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Effects of prescribed burning on mycorrhizal fungi in a pinus banksiana stand

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The Effects of Prescribed Burning on Mycorrhizal Fungi

in a *Pinus banksiana* Stand

by

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April 1997

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by Kyna A. Rigal

A Graduate Thesis Submitted In Fulfilment

of the Requirements for the

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A caution to the reader

This M.Sc.F. thesis has been through a formal process of review and commented on by at least three faculty members.

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Dedication

In loving memory of my Grandfather, Bernard Morris Alexandor, who taught me that all of my goals and aspirations are within my reach.

Abstract

The purpose of this study was to examine the effects of fire on mycorrhizal fungi in a *Pinus banksiana* stand. It was hypothesized that an optimal fire intensity leads to an increase in ectomycorrhizal colonization of crop species and to a decrease in vesicular-arbuscular mycorrhizal colonization of competition species.

Pinus resinosa seedlings grown in the greenhouse on soil from burned plots had significantly higher ectomycorrhizal colonization. There was no significant correlation between fire intensity and ectomycorrhizal colonization of the greenhouse *P. resinosa* or *Pinus strobus*.

The *P. strobus* out-planted on the Clearcut and scarification and the Scarified and Prescribe Burned Treatments had significantly higher colonization than both the *P. strobus* out-planted in the Clearcut Treatment and the *P. resinosa* at all Treatment levels. There were significant levels of interactions in all of the ectomycorrhizal studies. Neither the field planted *P. resinosa* nor the *P. strobus* had a significant correlation with fire intensity.

The relationship between fire intensity and vesicular-arbuscular mycorrhizal (VAM) colonization in *Trifolium repens* and *Agrostis palustris* grown and germinated on soil from a *P. banksiana* stand was inconclusive because the seeds from the four non-burned plots failed to germinate. There was no significant relationship between fire

intensity and VAM colonization.

Burned and non-burned field plots were examined for fungal carpophores one year after the prescribed fires. Thirty-seven fungi species were found: of these, 11 mycorrhizal fungi, nine saprophytic fungi, and two pathogenic fungi were identified. All of the pathogenic and saprophytic fungi were found on the burned plots while only two of them occurred on the non-burned plots. Five of the mycorrhizal fungi occurred on both the burned and non-burned plots, and two of them occurred exclusively on the non-burned plots.

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I would like to express a special thank you to my family for their support throughout my time at both Trent University and Lakehead University.

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Chapter 1:

A literature review of the effects of fire on soil fungi

Introduction

Before settlement by Europeans, fire was a dominant feature of most Canadian landscapes, with a recurrent passage every 10 to 10 000 years depending on soil, climate, topography, and fuel type (Anonymous 1987). The shortest fire frequencies were typical of the prairie, boreal and Great Lakes-St. Lawrence forest regions (Burgess and Methven 1977; Cwynar 1977; Frissell 1973; Heinselman 1981; Jones and DeByle 1985; Maissurow 1935; 1941; Methven and Murray 1974; Van Wagner 1970), whereas long frequencies were found in the coastal forests of British Columbia and in the arctic tundra (Payette *et al.* 1989; Wilton and Evans 1974). Clearly, most Canadian forests have evolved under the selective pressure of fire, leading to fire-adapted ecosystems. Recent fire suppression and silvicultural practices have modified these fire cycles which in turn have greatly affected ecosystem dynamics (Duchesne and Rigal 1995). To manage the forest in a sustainable manner it is imperative to examine these practices and changes in the ecosystem.

In recent years forest management, based on holistic or ecosystem approaches, has been emphasized as a measure to promote biodiversity conservation. One important

premise of this approach is that managed forests should maintain their biodiversity and their health even under repeated use. Fire, because of its regulatory role on pre-settlement biodiversity, should be used as a guide for forest management. Further, it is proposed that management of Canadian temperate and boreal forests could be conducted in a manner that emulates natural disturbance caused by fire. This approach stems from the widely accepted observation that wildfire was responsible for the maintenance of biodiversity in Canadian forests at the microsite, ecosystem, and landscape levels (Duchesne and Rigal 1995).

Recently, the impact of wildfire on soil microorganisms, such as algae, bacteria, and fungi has gained recognition (Herr *et al.* 1994; Widden and Parkinson 1975). These organisms are essential to ecosystem health, vigour, and productivity (Diaz-Ravina *et al.* 1993a; Wells *et al.* 1979). Ahlgren and Ahlgren (1965) suggested that intense fires, which may sterilize the soil, allowed for decreased competition and, therefore, resulted in an increase in subsequent microbial activity.

Whereas past research into this field provided some valuable insights into the effect of fire on soil microorganisms, the widespread use of Byram's formula, as described by Alexander (1982), offers an ideal tool to quantify fire behaviour. Byram's formula (1959), I = Hwr, describes fire intensity in terms of the heat of combustion (H) in kilojoules per kilogram, the weight of fuel consumed per unit area (w) in kilograms per square metre, and the rate at which fire spreads (r) in metres per second (Alexander 1982; Byram 1959). Intensity (I) is expressed in kilowatts per metre ($kW\ m^{-1}$). Although fire intensity cannot be directly compared to temperature, temperature in

combination with fire duration is accounted for in terms of energy released in Byram's formula.

The objective of this chapter is to review the impact of fire on soil fungi.

Fire and soil processes

In the absence of fire, soil microorganisms are the dominant decomposers (Diaz-Ravina *et al.* 1993b), however, fire is a rapid catalyst for this breakdown and nutrient release in forest soil. Fire is also considered to be one of the most important rock weathering processes (Wright and Heinselman 1973), and therefore aids in enriching the soil with essential mineral and nutrients that may not otherwise be available. Highly organic soils may have greater microbial densities in their deeper horizons than at the surface (Acea and Carballas 1990); thus the effect of fire on the soil profile would depend on fire severity, or depth of burn.

A surface or ground fire causes a succession of events; the organic layer is reduced to ash, soil pH is raised, and the concentration of soluble elements increases (Raison 1979). Fire may also initiate erosion since ash is easily removed from the site through water regimes and flow (Wells *et al.* 1979). Surface fires consume organic matter, increase the pH of the residual litter (Amaranthus and Trappe 1993; Bisset and Parkinson 1980; Feller 1982; Widden and Parkinson 1975), and increase the concentration of soluble elements in the soil (Amaranthus and Trappe 1993; Feller 1982; Petersen 1970). This change in both pH and element concentration in the soil may result in increased growth of soil microflora and microfauna. The amplitude of

these phenomena depends greatly on fire intensity (Herr *et al.* 1994). Fires with the greatest fertilization effect tend to be those with an intensity of approximately 10 000 $kW \cdot m^{-1}$ (Duchesne and Rigal 1995).

Although a myriad of nutrients are lost, from the site, through volatization and ash erosion (Wein and MacLean 1983), after fire, there is an immediate rise in soil fertility (Smith 1973; Springer 1988; Wade 1989). The increase in nutrients may initiate a delayed microflora flush. The effect of fire intensity on the extent of the nutrient flush is not entirely understood. Herr *et al.* (199) speculated that high fire intensities led to a smaller nutrient flush than fires of low intensity and Wein and MacLean (1983) suggested that nutrient loss correlated positively with fire intensity.

Fire severity, defined as the depth of the burn into the substrate, affects soil processes by the mere removal of biomass (Raison 1979). Among the volatilized organic matter is nitrogen, phosphorus, nitrogen fixing organisms, minerals, and other nutrients (Raison 1979). Harvey *et al.* (1979) suggested that organic matter aids in stabilizing pH, moisture, and temperature levels. Therefore, organic matter may play a key role in achieving optimum growth conditions for microorganisms by providing adequate microsites (Lucarotti *et al.* 1978).

Soil microbial biomass and species number decrease immediately following fire (Ahlgren and Ahlgren 1965; Deka and Mishra 1983; Jalaluddin 1969; Jorgensen and Hodges 1970; Meiklejohn 1955; Theodorou and Bowen 1982; Wright and Bollen 1961). This, in part, may be due to the actual combustion of the organic soil combined with heat sterilizing effects on non-charred area and subsequent moisture loss (Dunn *et*

al. 1985). The number of soil microbes decreases and increases at various rates over time depending on taxa. It has been speculated that the eventual rise in densities, over original values for all soil microorganisms, may be due to the inactivation of growth inhibitory substances by heat (Petersen 1970; Seaver and Clark 1910). It was hypothesised that the variation in microorganism population response is related to burn and post-burn litter and soil moisture levels (Ahlgren and Ahlgren 1965; Widden and Parkinson 1975).

The effects of fire on soil fungal populations

The response of fungal populations to fire depends on the nature of the fungi and the fire (Wright and Tarrant 1958). Fire behaviour is influenced by past and present weather conditions (Bisset and Parkinson 1980; Ahlgren and Ahlgren 1965; Harvey *et al.* 1979). In general, soil fungal populations decrease immediately after a burn (Meiklejohn 1955). Depending on the site, and its accompanying idiosyncrasies, fungal composition may also change following fire. For example, subsequent to bush-fires in Kenya, Meiklejohn (1955) observed that in two out of three sites sampled, the plate counts of *Penicillium* spores remained the same. In contrast, Widden and Parkinson (1975), found the count of *Penicillium* decreased with fire in a *Pinus contorta* stand in Alberta.

Tiwari and Rai (1977) observed a reduction of species of microfungi in India after a prescribed burn in May. They also found that fire influences microfungal species

richness and assemblages (Tiwari and Rai 1977) which was probably a consequence of differing heat tolerance levels. After a surface slash burn in India, the density of bacteria took only 20 days to return to their original level while fungal populations took one month (Deka and Mishra 1983). Similar results were found in both a Guinea savanna (Adedeji 1983) and an East Mediterranean ecosystem (Arianoutsou-Faraggitaki and Margaris 1982) where fungal populations required more time to return to their previous densities than did bacteria.

Following fire, there is a myriad of ways fungi repopulate a site. In the case of an incomplete burn, viable on-site spores can germinate. Fungi from areas adjacent to the fire can invade through the soil and spores from outside the burned area can be carried in by the wind or by animals (Widden and Parkinson 1975). In the case of volcanic disturbance, fungi can grow up through the tephra from underlying soil (Carpenter *et al.* 1987).

Burning can predispose a site to infection by certain fungi. Under natural conditions, phoenicoid, or fireplace fungi, have been found exclusively on heat treated substrates including burned forest ground (Petersen 1970), soil heated by steam (Warcup 1990), and fresh volcanic tephra mixed with organic material (Carpenter *et al.* 1987). There are several documentations of unique fungi appearing on site after both prescribed fire and wildfire (Warcup 1990; Carpenter and Trappe 1985; Widden and Parkinson 1975).

Following wildfire in South Australia, a new ectomycorrhizal fungal species, *Muciturbo reticulatus*, appeared in a eucalypt forest (Warcup 1990). New

ectomycorrhizal species were also observed in the Mount St. Helens volcano devastation zone (Carpenter *et al.* 1987). Fungal species were also found on the volcanic tephra which habitually appear after prairie or forest fires (Carpenter *et al.* 1987). Although many phoenicoid fungi do not interfere with tree growth, some are pathogenic. In a *Pinus contorta* stand in Alberta, fire was observed to promote favourable growth conditions for the pathogen *Cylindrocarpon destructans* (Widden and Parkinson 1975). The stimulation of the growth of *Rhizina undulata* is also observed to occur after fire (Callan 1993).

The phoenicoid fungus *Morchella conica* has received particular attention, presumably due to its economic value. In general, morels are widely distributed (McCubbin 1913; Buscot 1989), and are frequently found in a variety of forested sites in the absence of fire. However, after fire there is a prolific occurrence of morels. In a *P. banksiana* stand, *M. conica* fruited in May following a prescribed burn during the previous September (Duchesne and Webber 1993).

There are two main hypotheses explaining this unique fungal colonization after fire. Fungi such as *Rhizina undulata* and *Anthracobia melaloma* may depend on the heat generated during a fire to stimulate ascospore germination (Wicklow 1975; Carpenter and Trappe 1985). After fire the most numerous of the fungi may be from the order Ascomycotina because the ascospores tend to be more resistant to environmental factors than the conidia of the Fungi Imperfecti (Widden and Parkinson 1975). The second hypothesis is that fire may reduce competition, thus enabling carbonicolous fungi to pioneer (Carpenter and Trappe 1985; Wicklow and Hirschfield 1979).

Wicklow and Hirschfield (1979) hypothesized that early soil colonists exhibit a low tolerance to other soil microorganisms and would be short-lived. These fire adapted fungi presumably do not grow on site prior to the next natural fire (Wicklow and Hirschfield 1979).

Included in the phoenicoid fungi are various mycorrhizal fungi. The population and diversity of these types of fungi can be greatly influenced by fire (Herr *et al.* 1994; Visser 1995).

Vesicular-arbuscular mycorrhizal fungi

In the literature, vesicular-arbuscular mycorrhizal (VAM) fungi are the least abundant of the mycorrhizal fungi examined in context with fire. This may be due, in part, to the physical difficulties associated with the examination of VAM. Since outwardly, a VAM root looks the same as a non-mycorrhizal root, microscopic examination is necessary. Nonetheless, VAM fungi in the subdivision Zygomycotina are recognized as being important contributors to herbaceous plant growth.

After wildfire, in Spain, soils of adjacent non-burned plots were observed to have higher spore counts of VAM fungi than that of burned plots (Vilarino and Arines 1991). However, on the burned plots spore density of certain species increased only slightly. According to Widden and Parkinson (1975) and Wicklow and Hirschfield (1979), measuring fungal activity as a function of spore numbers on a site may be misleading, because, after a fire, fungal populations may be in an active mycelial stage;

thus spore counts would be low. Spores collected from non-burned plots had higher germination rates than those from the burned plots. In light of Widden and Parkinsons' (1975) hypothesis, one can conclude that the spores left on the non-burned site were the least viable. Similar to studies on algae and bacteria (Vazquez *et al.* 1993; White 1986) VAM infectivity was lower immediately after burning but then rose steadily (Vilarino and Arines 1991).

Ectomycorrhizal fungi

Although ectomycorrhizal fungi are recognized as important components of the temperate forest, very little is known about their response to fire (Browning and Whitney 1991; Herr *et al.* 1994; Villeneuve *et al.* 1989; Vogt *et al.* 1983). Ectomycorrhizae aid in water and nutrient uptake (Wright and Tarrant 1958) by roots and may even increase root resistance to pathogens (Harley and Smith 1983; Marx 1969; Zak and Wicklow 1980). Mycorrhizae, ectomycorrhizae in particular, may enhance root heat and cold tolerance (Hendrickson and Robinson 1982). Ectomycorrhizal fungi also play an essential role in nutrient cycling in the litter layer (Perry *et al.* 1989), and are therefore thought to reduce nutrient leaching (Parke *et al.* 1983).

Ectomycorrhizae continue to colonize roots throughout a tree's life (Visser 1995). Although colonization does not decrease with stand age, species composition does decrease. From the early-stage phoenicoid fungi to the late-stage fungi,

colonization remains constant (Danielson 1984a; Visser 1995). These fungi form intercellular networks of fungal hyphae in the cortex and epidermis of feeder roots of woody plants to form ectomycorrhizae. They live symbiotically with the feeder roots of the families: Pinaceae, Fagaceae, Betulaceae, Salicaeae, Juglandaceae, and Myrtaceae (Allen 1991; Marx 1991; Malloch and Malloch 1981) (Table 1). They are classified in the subdivisions Basidiomycotina and Ascomycotina (Perry *et al.* 1989). Ectomycorrhizae play a crucial role in the nutrient acquisition of their host plants (Read 1991; Soderstrom 1991) which in turn aids in competition between plants and microorganisms (Brundrett *et al.* 1990; Le Tacon *et al.* 1987; St. John and Coleman 1983). Hormonal relationships incurred by these fungal symbionts cause ectomycorrhizal roots to be physiologically active for longer periods than non-mycorrhizal roots (Ek *et al.* 1983; Ng *et al.* 1982; Slankis 1973). Under suitable environmental conditions, ectomycorrhizal trees benefit from enhanced water and nutrient uptake, increased resistance to root pathogens (Marx 1969; Sinclair *et al.* 1982), increased tolerance to water and temperature stress (Browning and Whitney 1991), and increased growth as compared to their non-mycorrhizal counterparts (Harley and Smith 1983; Herr *et al.* 1994; Trofymow and van den Driessche 1991).

There are several hypotheses explaining how the changes in soil chemical and physical properties after fire influence ectomycorrhizal growth. Similar to bacteria, soil ectomycorrhizal fungi may be favoured after a burn due to a hypothesized reduction of growth inhibitory substances (Herr *et al.* 1994; Widden and Parkinson 1975). It is also speculated that fire initiates a chemical alteration that may inhibit the growth of some

Table 1. Mycorrhizal status of plant species common to Ontario's boreal and St. Lawrence-Great Lakes forest types.

Species	Ectomycorrhizal fungi	Vesicular-arbuscular mycorrhizal fungi
Abies balsamea	✓	
Acer rubrum		✓
A. saccharum		✓
A. spicatum		✓
Agrostis spp.		✓
Alnus rugosa	✓	✓
Amelanchier sanguinea		✓
Aralia nudicaulis		✓
Betula papyrifera	✓	✓
B. alleghaniensis	✓	
Carpinus caroliniana	✓	
Carya ovata	✓	
Clintonia borealis		✓
*Comptonia peregrina**		✓
Coptis trifoliata		✓
Cornus canadensis		✓
Diervilla lonicera		✓
Fagus grandifolia	✓	
Fraxinus americana		✓
Juglans nigra	✓	✓
Larix laricina	✓	✓
Linnaea borealis		✓

Table 1 continued.

Species	Ectomycorrhizal fungi	Vesicular-arbuscular mycorrhizal fungi
*Maianthemum canadense**		✓
Oryzopisis asperifolia		✓
Ostrya virginiana	✓	
Picea glauca	✓	
P. mariana	✓	
*Pinus banksiana**	✓	
*P. resinosa**	✓	
*P. strobus**	✓	
Populus balsamifera	✓	✓
P. tremuloides	✓	✓
Prunus pensylvanica		✓
P. serotina		✓
*Pteridium aquilinum**		✓
Quercus alba	✓	
Salix humilis	✓	✓
S. nigra	✓	
Sorbus decora		✓
Thuja occidentalis		✓
Tilia americana	✓	
Trientalis borealis		✓
Trifolium repens		✓
Ulmus americana		✓

*Species found on The Frontier Lake Experimental Plots (Brundrett *et al.* 1990; Herr *et al.* 1994; Malloch and Malloch 1981).

fungi (Widden and Parkinson 1975) . The decrease in total soil nitrogen and phosphorus following fire may correlate with ectomycorrhizal formation since increased ectomycorrhizal formation is associated with low nitrogen and phosphorus concentrations (Trofymow and van den Driessche 1991).

Although fire increases soil pH and fungi tend to be favoured by more acidic soils (Widden and Parkinson 1975; Richards 1961), research found that ectomycorrhizal activity in the mineral soil increased slightly on a broadcast-burn clearcut in western Montana (Harvey *et al.* 1980). They also found that some ectomycorrhizae have the tenacity to survive up to 10 months after a clearcut despite the fact that root systems lose the ability to sustain ectomycorrhizal growth after their stems and tops are removed. In this case, the ectomycorrhizae were not numerous enough to inoculate introduced trees (Harvey *et al.* 1980). By the same token, other researchers suggest that fire may decrease soil ectomycorrhizal inoculum potential (Pliz and Perry 1983; Wright and Tarrant 1958). However, Pliz and Perry (1983) found more *Cenococcum* ectomycorrhizae per *Pseudotsuga menziesii* seedling on the clearcut and burned sites than in control plots.

It has been found that by manipulating the amount of organic layer on a site, the number of ectomycorrhizal species remained the same but richness and inoculum potential changed (Baar *et al.* 1993). It was also concluded that increased organic matter inhibits ectomycorrhizal fungi infectivity (Baar *et al.* 1993). Because fire decreases the amount of organic material on a site, it could be hypothesized that fire would not inhibit ectomycorrhizal fungal growth.

Soil attributes and fire intensity should be examined in context with soil microorganism response to fire, however, Herr *et al.* (1994) believed that fungi may have a host preference. In the Great Lakes-St. Lawrence forest region, on humo-ferric podzol, ectomycorrhizal infectivity correlated positively with fire intensity for *P. strobus* (Herr *et al.* 1994). In contrast, ectomycorrhizal infectivity failed to correlate with fire intensity for *P. resinosa* thereby suggesting host preference by ectomycorrhizal fungi (Herr *et al.* 1994).

Soil fungi as indicators of stand diversity

There has been limited research on soil fungi as indicators of stand diversity even though fungal diversity and numbers may be crucial indicators of overall stand health. The fungi present on the site may tell a story of the events, such as fire and disturbance, which lead up to the present stand composition and health. Fungal activity influences stand pH (Raubuch and Beese 1995) which in turn affects stand health. For example, stands with a plethora of root rot pathogens such as *Rhizina undulata* and/or *Armillaria mellea* would not be as healthy as stands with the ectomycorrhizal fungi *Laccaria laccata* and/or *Cantharellus cibarius*.

The kinds of interactions, balanced versus unbalanced, among saprophytes and symbiotic fungi are important in tree stand health and vigour. Fire and other disturbances undoubtedly play an important role in establishing the soil microorganism dynamic.

Microfungi assessment techniques

There are various techniques employed to examine soil algal, bacterial, and fungal populations. Due to the size and nature of some of these microorganisms, accurate observations can be difficult to make. Quantifying microorganisms in soil can be accomplished in terms of physiological activity (specifically respiratory) (Jorgensen and Wells 1971; Rippka 1988), biomass, richness, density, and numbers (Harvey *et al.* 1980). Changes in microsite environmental conditions may affect the nature of the microorganisms, and so upon sampling, steps must be taken to avoid drying, heating, and microbial contamination (Diaz-Ravina *et al.* 1993b).

There are many approaches used in assessing soil fungal populations. These include measuring the number, mass, and density of propagules, propagule viability (Vilarino and Arines 1991), observing the presence/absence of fruiting bodies (Carpenter *et al.* 1987; Mayfield and Wade 1993), and determining species richness and diversity. Usually, soil cores are used to assess soil fungi (Lucarotti *et al.* 1978; Acea and Carballas 1990; Tiwari and Rai 1977; Morrall and Vanterpool 1968; Vazquez *et al.* 1993). However, to determine mycorrhizal status the removal of plant roots provides a convenient assessment technique (Herr *et al.* 1994).

The extent of ectomycorrhizal root formation is assessed by determining, with a dissecting microscope, the proportion of ectomycorrhizal root tips in a given distance of root (Danielson 1984a; Herr *et al.* 1994; Marx 1969). VAM assessment requires the clearing and staining of the roots prior to examination (Brundrett *et al.* 1984;

McGonigle *et al.* 1990). Chlorazol black E is an ideal stain for showing details of internal hyphae, vesicles, and arbuscules (Brundrett *et al.* 1984). Since vesicles and hyphae can be produced in roots by non-mycorrhizal fungi, arbuscular colonization is the most reliable reflection of the root mycorrhizal status (McGonigle *et al.* 1990). To maintain objectivity, the line-intersect method is used to quantify mycorrhizal colonization (Brundrett 1984; Johansson 1994; McGonigle *et al.* 1990).

Conclusion

Forest researchers should recognize the importance of all aspects of a forest ecosystem. Soil microorganisms and fire are essential components of the temperate forest and, in comparison to their importance, have seldom been studied collectively in Canada's forests. The continuation of research that better defines fire and mycorrhizal fungi interactions is critical to aid in ensuring sustainable forest management.

In the future, with the use of Byram's forest fire intensity formula, achieving a better characterization of the effect of fire on soil diversity and soil processes is possible and highly desirable (Duchesne and Rigal 1995). With this further research, insights may be provided into the effects of fire control practices on soil microorganisms.

Chapter 2:

The effects of prescribed burning on ectomycorrhizal colonization in a *Pinus banksiana* stand

Introduction

In Canada, prescribed burning is a widely accepted silvicultural tool that is used for post-harvest site preparation (Kayll 1963; Weber and Taylor 1992). Between 1990 and 1993, 171 554 ha were prescribed burned for silvicultural purposes across Canada (Haddon pers. com. 1995). Alternate uses of fire include preparation of suitable seedbeds for natural or broadcast seeding, reduction of wild fire hazards (Weber and Taylor 1992), reduction of soil pathogens (Weber and Taylor 1992), management of competing vegetation (Buckman 1964; Weber 1990), facilitating post-harvest access for planters and machinery, and providing suitable habitat for a variety of wildlife species (Stein *et al.* 1992). Prior to the advent of organized fire suppression, after the turn of the 19th century, wildfire played a critical role in the Canadian forest landscape (Van Wagner 1990). Therefore, from an ecological perspective, fire plays a unique and necessary role in forest management.

Whereas considerable research has emphasized the effects of fire intensity on the regeneration of crop trees (e.g. Weber *et al.* 1987), the effects of fire on other groups of organisms, particularly soil microflora and microfauna, are not well understood

(Ahlgren and Ahlgren 1960; Visser 1995). It is critical to study soil microfauna and microflora in association with fire because they are the rudimentary control agents in the decomposition of organic matter and nutrient turnover rates that influence ecosystem stability and recovery following disturbance (Atlas and Bartha 1981; Herr *et al.* 1994; Paul and Clark 1989; Perry *et al.* 1989).

Phoenicoid fungi are pioneer colonizers of forest sites following disturbance by fire and comprise a large number of species from different taxonomic groups (Carpenter and Trappe 1985). These fungi play an important role in nutrient cycling and mobilization in fire-disturbed ecosystems (Carpenter and Trappe 1985; Carpenter *et al.* 1987). Moreover, they may contribute to plant growth and survival through mycorrhizal symbioses (Carpenter *et al.* 1987; Danielson 1984b). Ectomycorrhizal colonization, seedling health, and seedling survival increased with prescribed fire for *P. strobus* and seedling survival increased for *P. resinosa* in a *P. banksiana* ecosystem (Herr *et al.* 1994). Regardless of type of disturbance, young pines are colonized by ectomycorrhizae three to four months after germination (Allen 1991). When ectomycorrhizal colonization was compared between *P. banksiana* stands of 6, 41, 65, and 122 years, it was found that ectomycorrhizal colonization did not decrease with stand age, and that the number of mycorrhizal morphotypes increased with stand age (Visser 1995). Thus ectomycorrhizal fungi are an integral component of stands of any age, including the stand-initiation phase. The objectives of this study were: 1) to determine the effects of prescribed burning, scarification, and clearcutting on ectomycorrhizal root colonization of *P. resinosa* and *P. strobus* seedlings; and 2) to

examine the relationship between fire intensity and ectomycorrhizal colonization of these pine species.

Materials and Methods

Study site

The study area is located five kilometres east of the Petawawa National Forestry Institute at latitude 46°00' N and longitude 77°33' W in a *P. banksiana* stand within the Middle Ottawa section (L.4c) of the Great Lakes-St. Lawrence Forest region (Herr *et al.* 1994; McAlpine 1995; Rowe 1972). The site is relatively flat, with a difference in elevation of approximately four metres over one kilometre (Herr *et al.* 1994; McAlpine 1995). The overstory at the study site consisted of *P. banksiana* with 505 stems per hectare (ha^{-1}), *P. resinosa* with 50 stems ha^{-1}, and *P. strobus* with 100 stems ha^{-1} (Herr *et al.* 1994). The understorey had a density of 40 000 seedlings ha^{-1} of *P. strobus* (Herr *et al.* 1994). Herr *et al.* (1994) have given a detailed description of stand composition and soil attributes.

In the summer of 1990, an area of 150 metres by 1000 metres was clearcut and the residual slash (limbs and treetops) left in place (Figure 1). The cut-over area and the standing timber area was then divided into 40 plots, each measuring 35 metres by 70 metres, and each plot was divided by eight metre wide roads which served as fuel-breaks (Herr *et al.* 1994). Ten of the clearcut plots were burned-over in 1991 under five different levels (Herr *et al.* 1994) of the Canadian Forest Fire Weather Index (FWI) System (Table 2) (Van Wagner and Pickett 1985; Van Wagner 1987) (Figure 2).

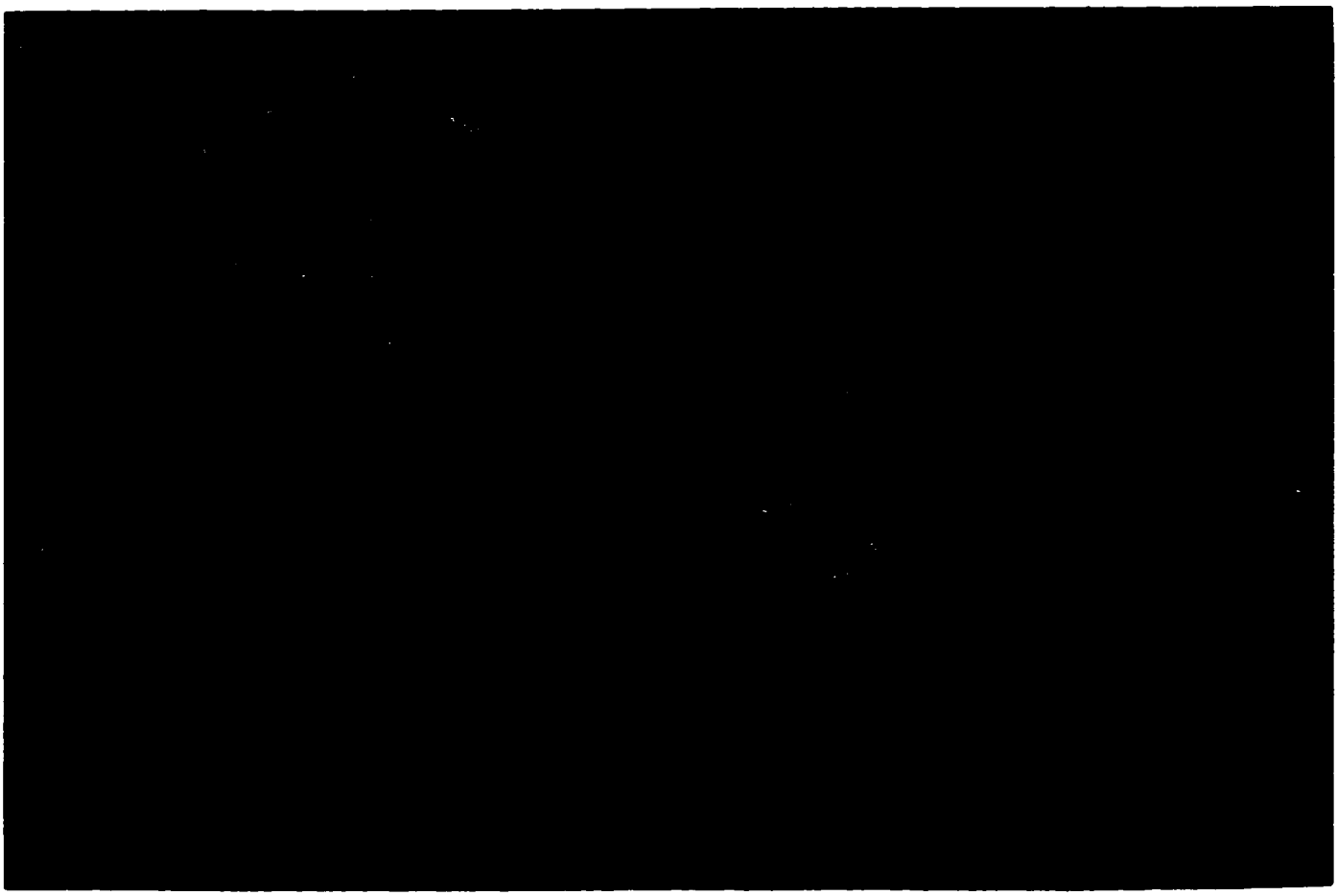


Figure 1. Aerial photograph of the Frontier Lake Experimental Site.

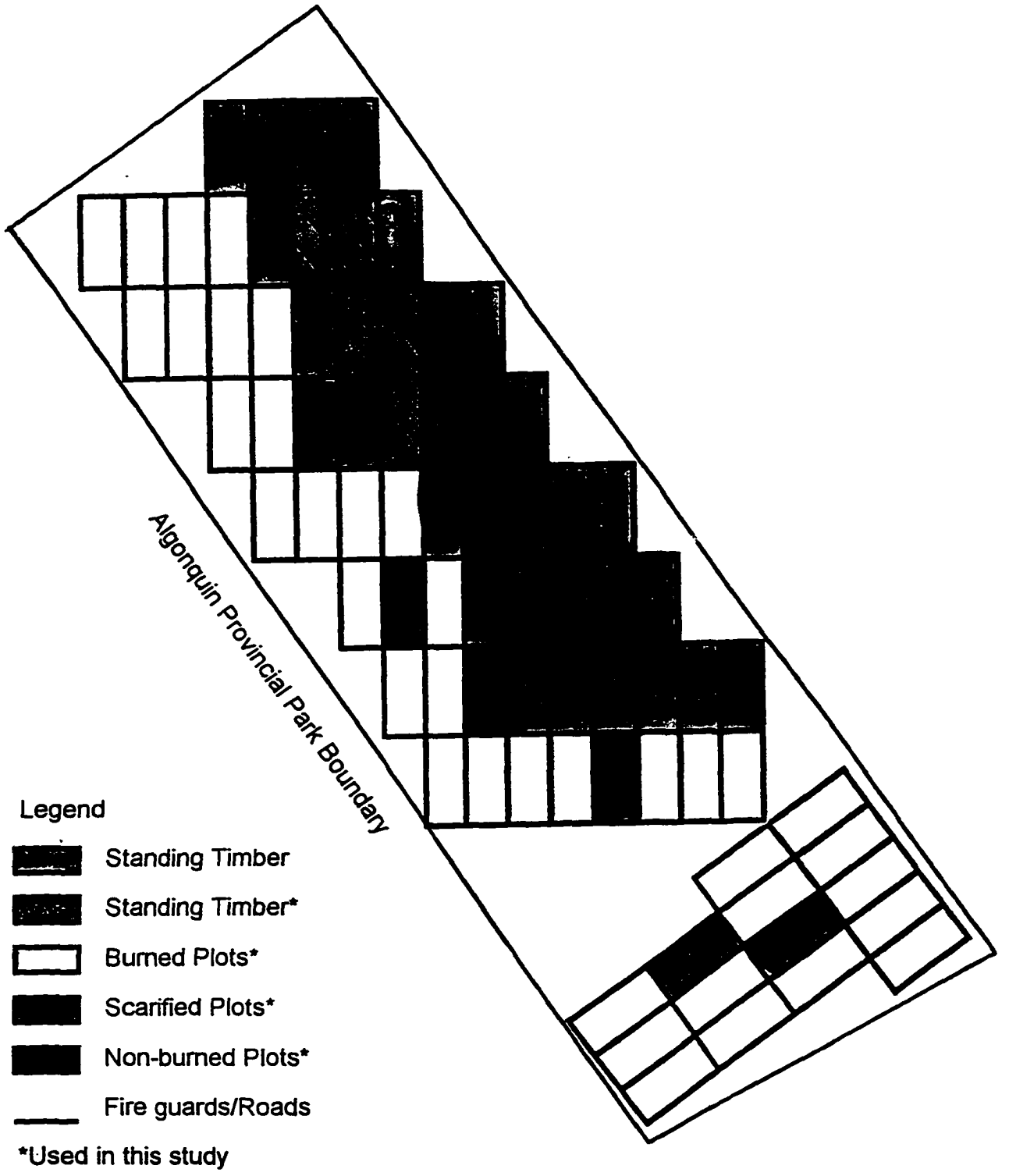


Figure 2. Diagram of the Frontier Lake Experimental Research Site.

Table 2. FWI* and Fire Intensity for each 35 metre by 70 metre, burned-over clearcut plot at Frontier Lake Experimental Site.

Date (1991)	FWI	Fire Intensity ($kW \cdot m^{-1}$)
14 June	18	10,143
14 June	18	19,854
24 June	22	2,097
24 June	22	11,077
10 July	7	4,132
10 July	7	11,176
12 July	14	5,565
12 July	14	17,259
8 August	6	446
8 August	6	1,063

*FWI: Fire Weather Index
(Herr *et al.* 1994)

Weber *et al.* (1987) indicate that the range of fire intensities optimal for the regeneration of *P. banksiana* can be up to 20 000 kW/m. Intensities experienced in this study are within this broad range. McAlpine (1995) has given full documentation on prescribed fire methods, burning conditions, and fuel consumption. Half of the remaining non-burned plots were scarified. In the present study ten clearcut and burned plots, three clearcut and scarified, and three clearcut plots were examined.

To examine the effects of fire within standing timber, 16 three metre by three metre plots were established with a quatre metre wide fire guard. In 1993,13 of these plots were burned under different fire intensities (Table 3). These fires were ignited by gasoline line ignition. After the sites were cleared of any fuel they were then loaded with a predetermined fuel load. Slash consumption was determined as the difference between the pre-burn and the post-burn fuel load. Depth-of-burn pins (McRae 1979) were used to determine organic material consumption. On-site weather conditions during prescribed burns were monitored with an automatic fire weather station to determine the component codes and indices of the FWI System (Anonymous 1987; Van Wagner 1987). Wind was closely monitored on a minute-by-minute basis to correlate with the resultant fire behaviour. The rate of spread of the fire was measured with a pin grid network on each plot; fire arrival time at each pin was recorded to provide distance and time information. Fire intensity was calculated using Byram's formula (1959).

All of the clearcut plots were planted with two-year-old, container-grown, non-mycorrhizal seedlings of *P. resinosa* and *P. strobus* in the first week of May 1992 (Herr

Table 3. FWI*, fire intensity, and species for each standing timber, three metre by three metre, burned-over plot at Frontier Lake Experimental Site.

Date (1993)	FWI	Fire Intensity ($kW \cdot m^{-1}$)	Species Examined
24 June	19	544	*P. strobus*
25 June	18	126	*P. strobus*
30 June	16	127	*P. resinosa*
5 July	16	10	*P. resinosa* *P. strobus*
5 July	16	96	*P. resinosa*
6 July	12	241	*P. resinosa*
6 July	13	432	*P. strobus* *P. resinosa*
9 July	22	55	*P. strobus*
13 July	14	175	*P. resinosa* *P. strobus*
21 July	26	186	*P. strobus*
23 July	11	796	*P. resinosa* *P. strobus*
28 July	4	100	*P. resinosa* *P. strobus*

*FWI: Fire Weather Index

et al. 1994). Half of each plot was planted with *P. resinosa* and the other half was planted with *P. strobus*. The seedlings were spaced at two metre by two metre intervals. The root systems of five seedlings of each species were examined at the time of out-planting to ensure that no ectomycorrhizae were present (Herr *et al.* 1994).

Ectomycorrhizae assessment

Field study

To assess root colonization by ectomycorrhizal fungi, seedlings from the clearcut area were harvested, in July 1994, two years following planting. Three seedlings of each species were harvested from each of the ten burned-over plots, from three of the non-burned clearcut plots, and from three of the non-burned clearcut scarified plots. At harvest, healthy seedlings showing leader growth with no signs of browning were randomly selected within the plots and lifted from the ground with a tree planting spade (Herr *et al.* 1994). Care was taken not to break off small roots during harvesting. The seedlings were stored in glass jars containing 50 percent (v/v) ethanol and water and refrigerated at approximately two degrees Celsius until analyses were conducted in April and May 1995.

Colonization by ectomycorrhizal fungi was assessed using a modification of the method of Marx (1969) as shown in Herr *et al.* (1994). Fifty, three centimetre, root segments from each seedling were randomly selected and were assessed for colonization with a Zeiss DR photodissecting microscope. However, where there were not enough root sections, as many as possible were taken with a minimum of 30. The total number of lateral roots of each segment was determined and classified as ectomycorrhizal and

non-ectomycorrhizal. Monopodial, single dichotomies, and two or more dichotomies were also counted as ectomycorrhizal root tips (Figure 3 and 4). If root ectomycorrhizal status was questionable, the sample was hand sectioned (Figure 5). The results for each seedling were expressed as the percentage of mycorrhizal root tips (number of ectomycorrhizal root tips / total number of laterals).

Greenhouse study

To assess ectomycorrhizal formation on germinating seedlings, two 20 centimetre diameter soil cores, from the three metre by three metre burns were planted with ten *P. resinosa* and ten *P. strobus* seeds on June 24, 1994. The soil cores were placed in fifteen centimetre diameter plastic pots. The *P. resinosa* seeds were from Algonquin Park and Cedar Lake (Appendix A). The *P. strobus* seeds were from the Petawawa National Forestry Institute (Appendix A). Soil cores were also taken from four plots that did not receive burn treatment. The *P. strobus* seeds were stratified for thirty days, from May 27 to June 24 1994. *P. resinosa* required no stratification and the seeds were therefore planted directly, by hand, in the soil cores for germination (Creasey and Myland 1993). Seedlings grew for 135 days before they were harvested on November 15, 1994. Standard greenhouse conditions consisted of a 14 hour photoperiod with an ambient temperature of 22 degrees Celsius and 75 percent relative humidity. The soil cores were maintained at 22 degrees Celsius and had 27 percent average moisture content. The seedlings were watered once every three days. Ectomycorrhizal colonization was assessed in the same manner as in the field study.

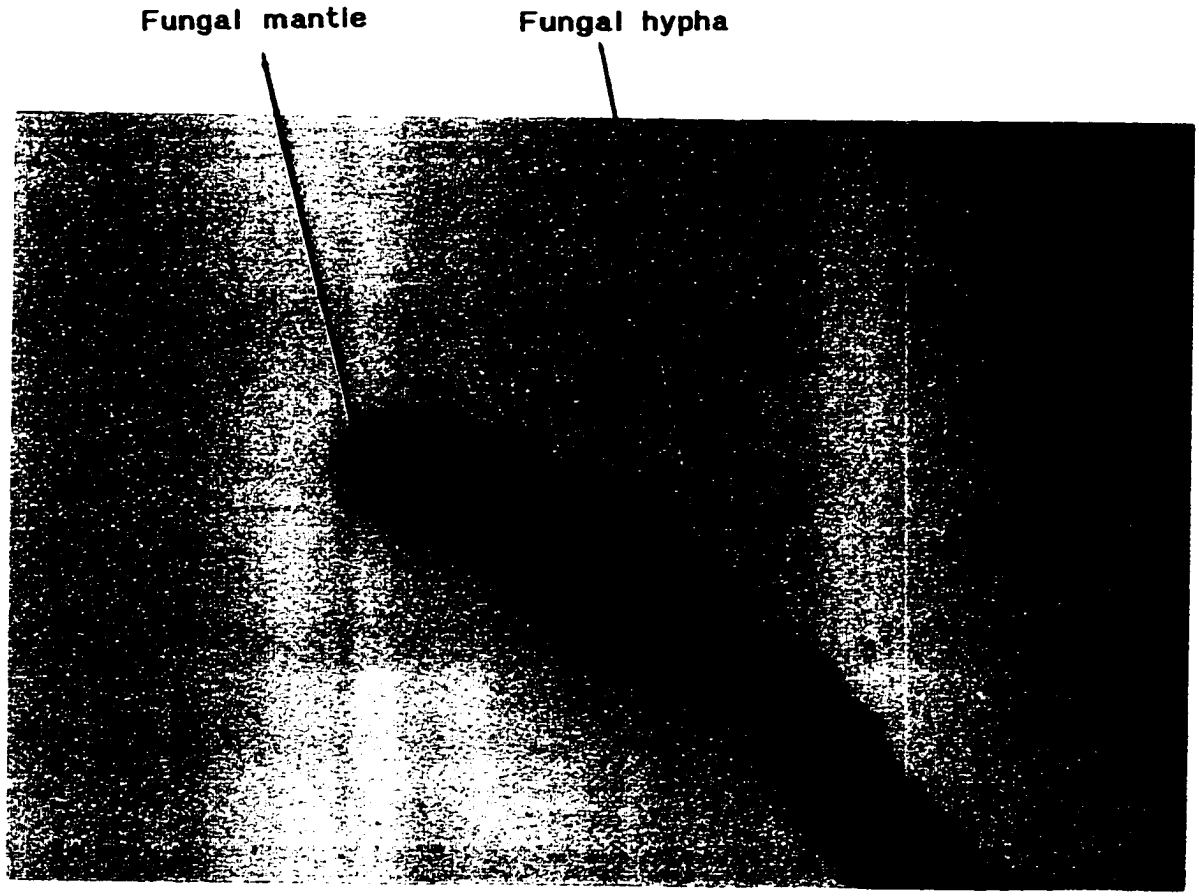


Figure 3. An example of a monopodial ectomycorrhizal root tip.

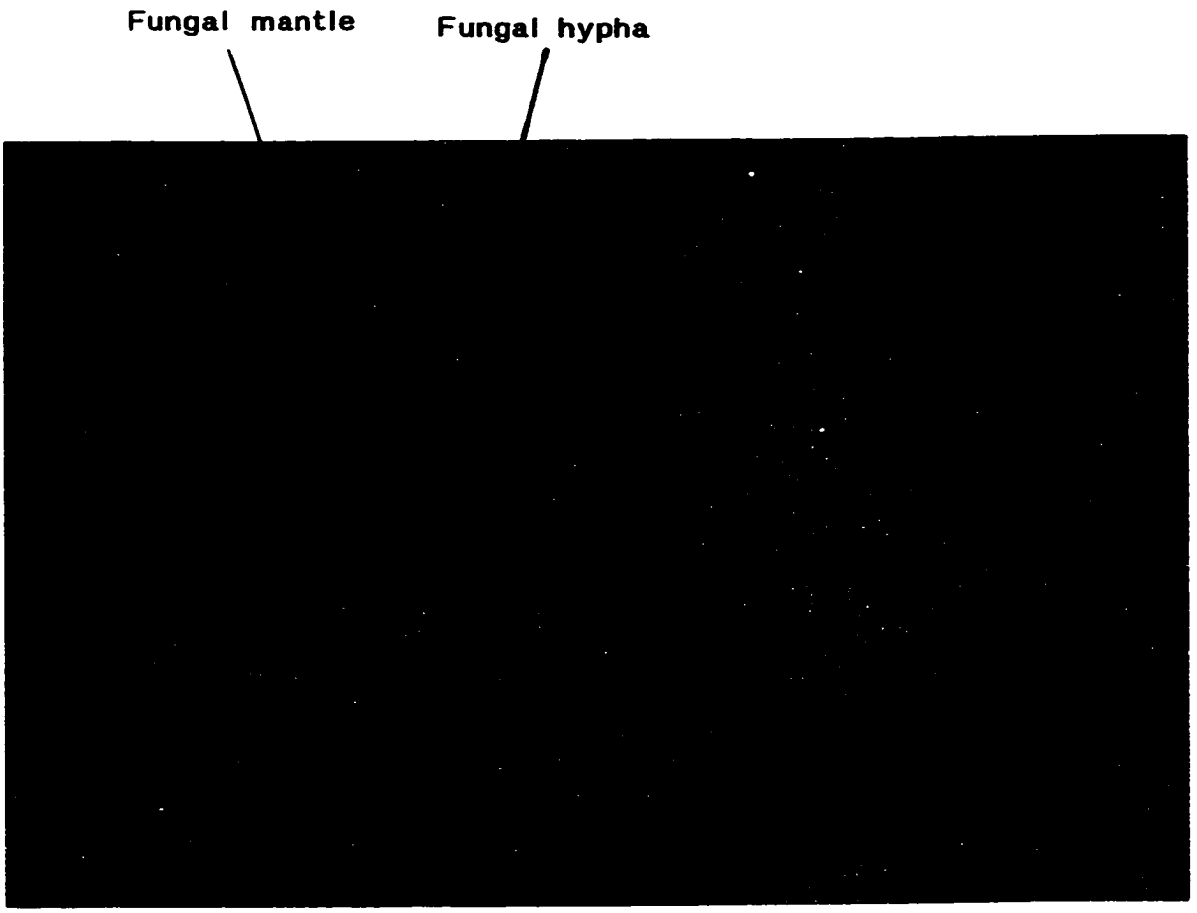


Figure 4. An example of a dichotomized ectomycorrhizal root tip.

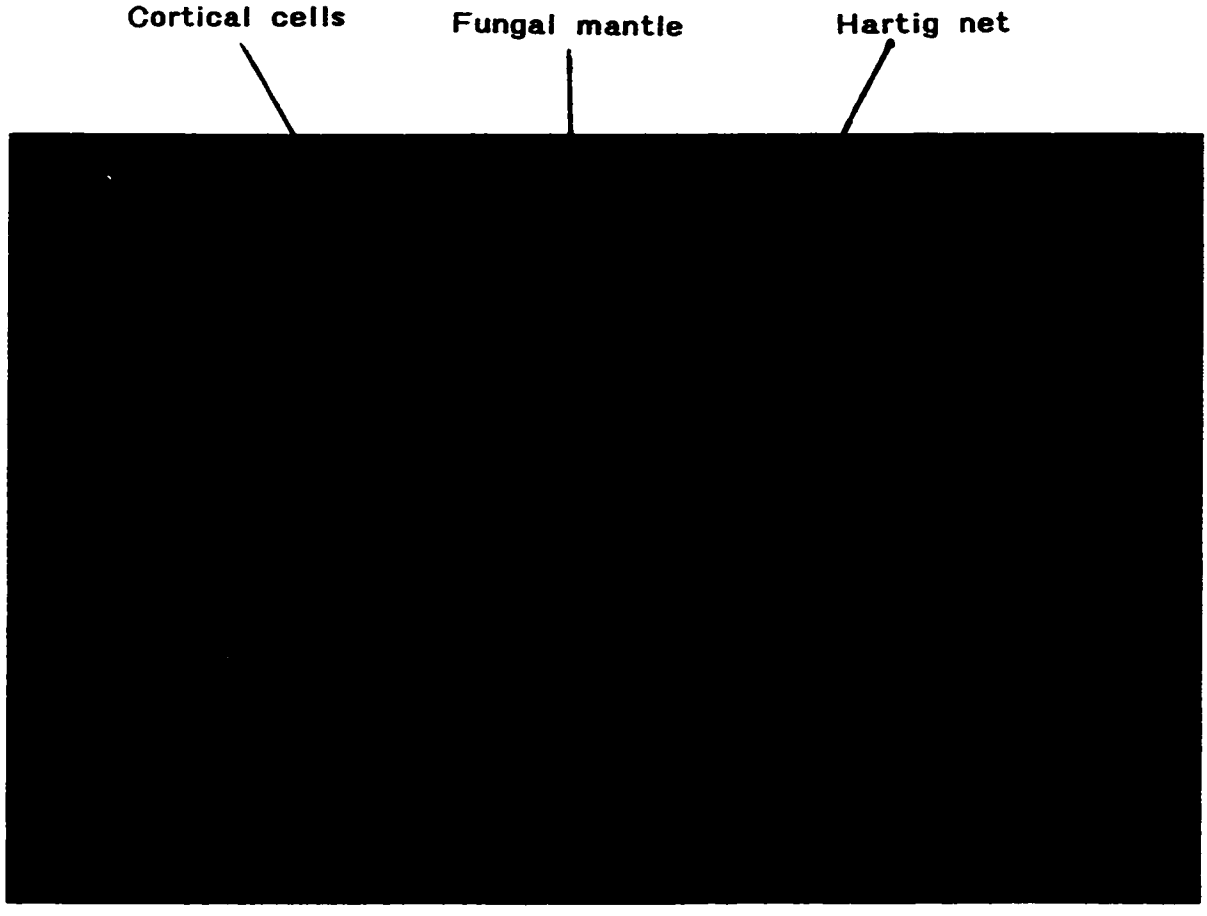


Figure 5. An example of a hand sectioned ectomycorrhizal root tip.

Statistical analyses

Analyses of the field and greenhouse study were performed separately (Equations 1, 2, and 3). For correlation and regression analyses all of the data were transformed. The log(x+1) transformation, where x is percent ectomycorrhizal colonization, resulted in the residuals having the lowest variance and a symmetric distribution. Correlation of ectomycorrhiza formation with fire intensity and pre-fire fine fuel moisture content was investigated using Pearson's matrix. Mixed analysis of variance was performed using Type III sums of squares. This analysis was followed by post hoc multiple comparisons using Scheffe's test. Scheffe's is the most conservative of the post hoc tests and was chosen because of the large number of tests conducted. Scheffe multiple comparisons test was used to examine differences in means in colonization between scarified plots, burned-over plots, and non-burned plots. Differences in colonization of seedlings grown in a burned-over substrate and a non-burned substrate were determined using the same process. The alpha-level for rejecting null hypotheses was set at α=0.01 due to the extensive testing, the large sample size, and to attempt to avoid a Type I error. All analyses were conducted using SPSS 6.1 (1994) and SAS.

$$Y_{ijklmnn} = \upsilon + T_i + \omega_{(i)j} + \zeta_{(ij)} + P_k + TP_{ik} + \omega P_{(i)jk} + \varepsilon_{(ijk)l} + S_{(ijkl)m} + r_{(ijklm)n}$$

i: 1,2,3 $j_{(1)}$: 1,2,..,10 *k*: 1,2 *l*: 1 *m*: 1,2,3 *n: 1,2,...,50*
$j_{(2)}$: 1,2,3
$j_{(3)}$: 1,2,3

where:

$Y_{ijklmnn}$	=	the ratio of the number of ectomycorrhizal root tips divided by the total number of root tips of the n^{th} root section from the *m*th seedling of the *kth* species of the *jth* plot of the *ith* treatment
υ	=	the overall mean
T_i	=	the fixed effect of the *ith* treatment
$\omega_{(i)j}$	=	the random effect of the *jth* plot within the *ith* treatment
$\zeta_{(ij)}$	=	restriction error*
P_k	=	the fixed effect of the *kth* species
Tp_{ik}	=	the interaction of the *ith* treatment with the *kth* species
$\omega P_{(i)jk}$	=	the interaction of the *kth* species with the *jth* plot within the *ith* treatment
$\varepsilon_{(ijk)l}$	=	sub-plot error
$S_{(ijkl)m}$	=	the random effect of the *mth* seedling within the *kth* species within the *jth* plot within the *ith* treatment
$r_{(ijklm)n}$	=	the random effect of the *nth* root section within the *mth* seedling within the *kth* species within the *jth* plot within the *ith* treatment (*Anderson 1970).

Equation 1. Linear model for *P. resinosa* and *P. strobus* field study.

Linear model for *P. resinosa* laboratory study:

$$Y_{ijk} = U + T_i + P_{(i)j} + r_{(ij)k}$$

i: 1,2 $\quad j_{(1)}$: 1,2 $\quad k$: 1,2,...,50

$j_{(2)}$: 1,2,..8

Linear model for *P. strobus* laboratory study:

$$Y_{ijk} = U + T_i + P_{(i)j} + r_{(ij)k}$$

i: 1,2 $\quad j_{(1)}$: 1 $\quad k$: 1,2,...,50

$j_{(2)}$: 1,2,..,10

where:

Y_{ijk}	=	the ratio of the number of ectomycorrhizal root tips divided by the total number of root tips of the *kth* root section from the *jth* pot from the *ith* treatment
U	=	the overall mean
T_i	=	the fixed effect of the *ith* treatment
$P_{(i)j}$	=	the random effect of the jth pot within the *ith* treatment
$r_{(ij)k}$	=	the random effect of the *kth* root section within the *jth* pot within the *ith* treatment

Equation 2 and 3. Linear models for *P. resinosa* and *P. strobus* laboratory studies.

Results

Field study

The *P. strobus* out planted on the Clearcut and Scarified and the Clearcut and Prescribe Burned Treatments had significantly higher colonization than both the *P. strobus* out-planted in the Clearcut Treatment and the *P. resinosa* at all Treatment levels (Table 5). There were significant levels of interactions in all of the ectomycorrhizal studies (Table 4). Neither the field planted *P. resinosa* ectomycorrhizal colonization nor the *P. strobus* ectomycorrhizal colonization had a significant correlation with fire intensity. No significant correlation was found between fire intensity and *P. resinosa* and *P. strobus* percent ectomycorrhizae (Figures 6 and 7).

Greenhouse study

P. resinosa germinated in only ten of the 17 pots, containing soil cores, from the experimental plots and *P. strobus* germinated in only 11 pots from the experimental plots. The two species were analysed separately because survival overlapped in only five of the pots.

P. resinosa ectomycorrhizal colonization was significantly affected by fire (Table 6), but there was no significant difference for *P. strobus* (Tables 7 and 8). However, neither *P. resinosa* nor *P. strobus* percent ectomycorrhizae correlated significantly with fire intensity (Figures 8 and 9).

Table 4. Analysis of variance of percentage of mycorrhizal root tips by site preparation treatment and species.

Source	df	SS	MS	MS-ratio	Conclusion re: H_o[a]
site prep. treatment	2	24.27	12.14	3.37	n.s.
whole plot error	13	46.79	3.6	no test	
restriction error	0	no est.	no est.	no test	
species	1	9.52	9.52	5.80	*
site prep. x species	2	24.02	12.01	7.32	**
whole plot error x species	13	21.36	1.64	no test	
subplot error	0	no est.	no est.	no test	
between seedlings within subplots	57	57.03	1.00	13.37	**
between roots within seedlings within subplots	4116	307.94	0.075	no test	
corrected total	4204				
mean	1				
missing data	89				
raw total	4294				

[a]Interpret the symbols in this column as follows: n.s. means "not significant - accept the null hypothesis" *means significant at the $\alpha = 0.05$ level, **means significant at the $\alpha = 0.01$ level.

Table 5. The means for percent ectomycorrhizl colonization of four year old *P. resinosa* and *P. strobus* seedlings in prescribed burned, clearcut, and scarified sites.

	mycorrhizal colonization (%)		
Species	Clearcut	Clearcut & Scarification	Clearcut & Prescribe Burned
P. resinosa	48.0a n*=400	44.6a n=398	52.4a n=1332
P. strobus	35.0b n=439	67.9c n=422	74.2c n=1312

*n=the number of root sections.

Note: means with the same letter are not significantly different.

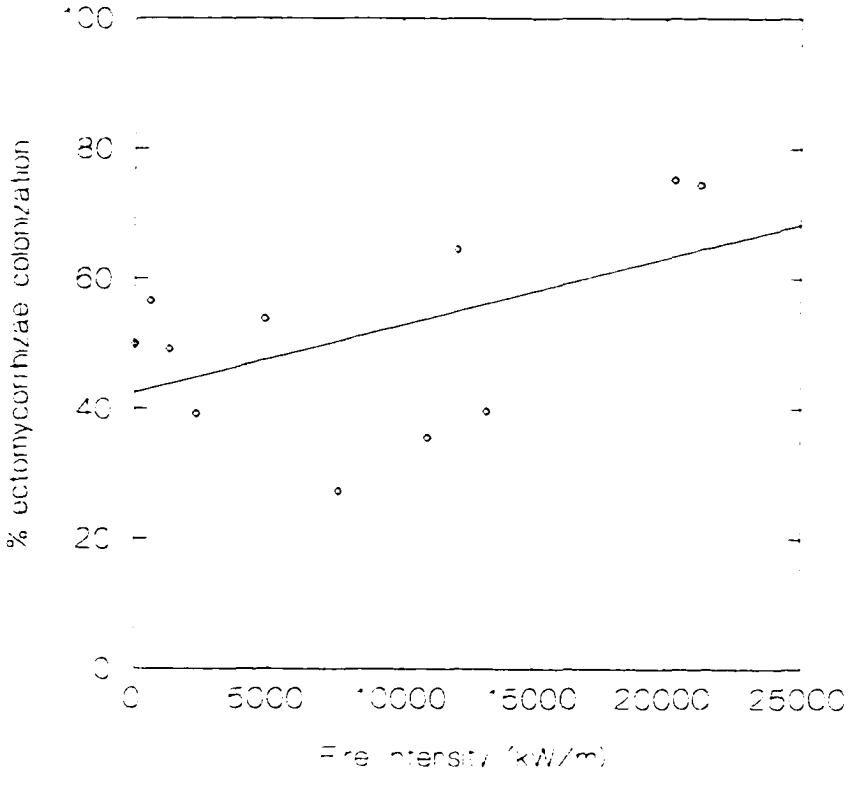


Figure 6: The relationship between fire intensity and percent ectomycorrhizal root formation in field *P. resinosa*.. The correlation between % ectomycorrhizal colonization and fire intensity is not significantly different from zero.

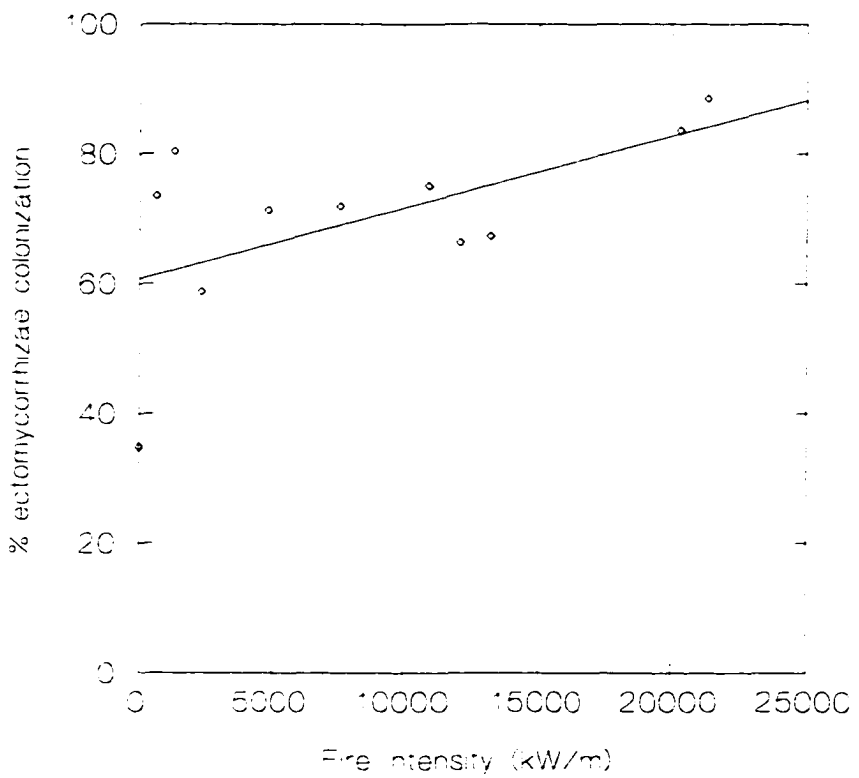


Figure 7. The relationship between fire intensity and percent ectomycorrhizal root formation in field *P. strobus*. The correlation between % ectomycorrhizal colonization and fire intensity is not significantly different from zero.

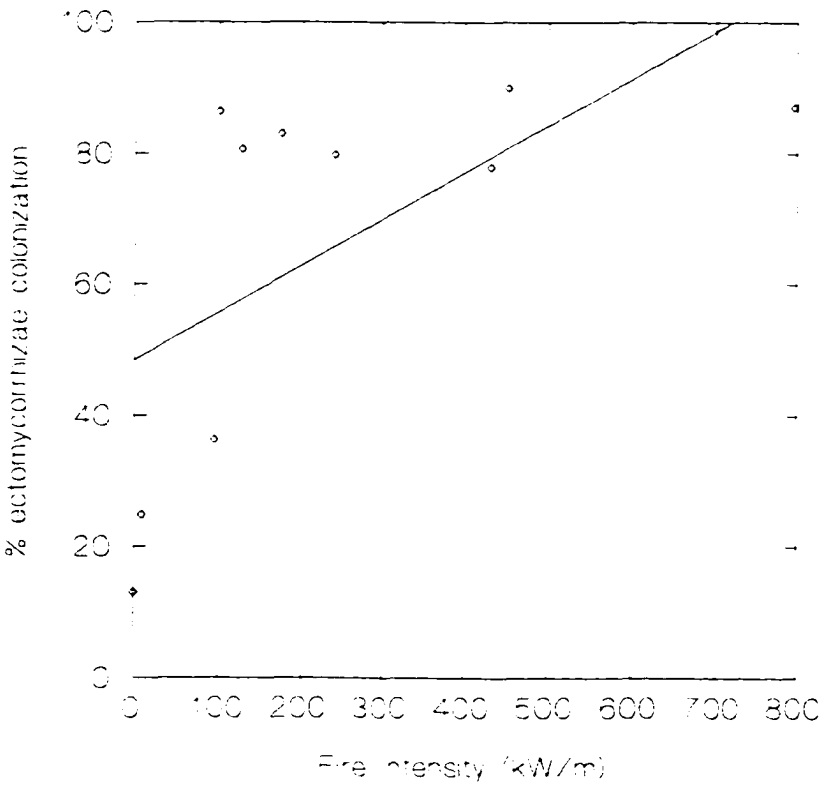


Figure 8. The relationship between fire intensity and percent ectomycorrhizal root formation in *P. resinosa* seedlings germinated and grown on burned substrate. The correlation between % ectomycorrhizal colonization and fire intensity is not significantly different from zero.

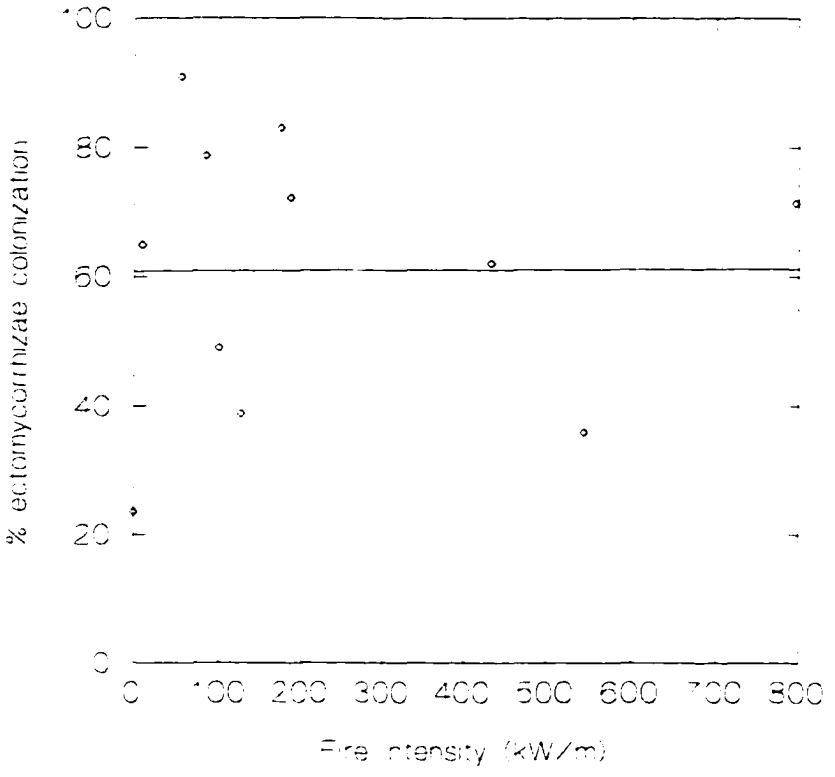


Figure 9. The relationship between fire intensity and percent ectomycorrhizal root formations in *P. strobus* seedlings germinated and grown on burned substrate. The correlation between % ectomycorrhizal colonization and fire intensity is not significantly different from zero.

Table 6. Analysis of variance of percentage of mycorrhizal root tips for *P. resinosa* by site preparation treatment.

Source	df	SS	MS	MS-ratio	Conclusion re: H_o
Treatment	1	22.39	22.3	9.60	*
Pot	8	18.63	2.33	35.99	*
Roots	448	28.99	0.065	no test	
Total	557				

*significant at the $\alpha = 0.01$ level.

Table 7. Analysis of variance of percentage of mycorrhizal root tips for *P. strobus* by site preparation treatment.

Source	df	SS	MS	MS-ratio	Conclusion re: H_o[a]
Treatments	1	10.00	10.00	6.99	n.s.
Pots	9	12.87	1.43	15.76	*
Roots	501	45.47	0.90	no test	
Total	592				

[a]Interpret the symbols in this column as follows: n.s. means "not significant - accept the null hypothesis".
*significant at the $\alpha = 0.01$ level.

Table 8. Means for percent ectomycorrhizal colonization for seedlings of *P. resinosa* and *P. strobus* grown on burned substrate and non-burned substrate.

Species	Burned-over substrate	Non-burned substrate
P. resinosa	71.8a n*=598	13.1b n=112
P. strobus	64.5A n=612	23.5A n=62

*n=the number of root sections

Note: means with a different lowercase letter are significantly different for *P. resinosa* at a probability level of α=0.05. Means with the same capital letter are not significantly different for *P. strobus* at a probability level of α=0.05. There are no between species comparisons in the greenhouse study.

Discussion

In the greenhouse study with the 135 day old seedlings *P. resinosa* colonized more quickly than the *P. strobus* and in the field study with the four year old seedlings *P. strobus* had greater colonization than *P. resinosa* except on the clearcut site (Tables 5 and 8). Herr *et al.* (1994) also found that *P. resinosa* was colonized more rapidly, and to a greater extent, than *P. strobus*. This difference may be due to the variation in actual growth conditions, in growth requirements for *P. resinosa* and *P. strobus* (Burns and Honkala 1990; Nadelhoffer *et al.* 1983) and the site idiosyncrasies. Both groups of seedlings for the field and the greenhouse study were grown in zero percent cover, or 100 percent light. *P. strobus* is more shade tolerant than *P. resinosa* (Burns and Honkala 1990). Whereas *P. resinosa* requires fire for natural regeneration, *P. strobus* germination can be ameliorated by a shaded seedbed (Burns and Honkala 1990). The Frontier Lake experimental research site was initially dominated by *P. banksiana* (Figure 1); thus the area may not provide optimal growing conditions for either of the two tree species nor the ectomycorrhizal species.

Further, ectomycorrhizal colonization depends on both tree and fungal species (Browning and Whitney 1993). Although ectomycorrhizal fungi of the pines are similar, some are better suited for one species than others (Browning and Whitney1993). For example, *Laccaria proxima* mycorrhizae enhance the drought

tolerance of *P. banksiana* to a greater extent than do either *Thelephora terrestris* or *Laccaria bicolor* (Browning and Whitney 1993). Since the results of this study are derived from a stand that is predominantly *P. banksiana*, the ectomycorrhizal fungi present in the soil for that species may dominate (Table 1).

The literature supports the finding that, for the greenhouse *P. resinosa* and the out-planted *P.strobus*, ectomycorrhizal root colonization increases in post-fire communities (Herr *et al.* 1994; Visser 1995). The lack of significance for the field *P. resinosa* and the greenhouse *P. strobus* in the level of ectomycorrhizal colonization after fire, as observed in this study (Tables 5 and 8) may be related to the depth of organic matter. Ectomycorrhizal fungi do not flourish in thick, nitrogen-rich organic layers (Baar and Kuyper 1993). This observation supports the low level of colonization in the *P. strobus* out-planted in the Clearcut (Table 5). One year after a reduction in humus layer, species richness of ectomycorrhizal fungi and fruiting bodies can increase significantly (De Vries *et al.* 1995). However, this effect can decrease in subsequent years to minimal values (De Vries *et al.* 1995). An allelopathic response of seedling ectomycorrhizae to forest litter has also been reported (Alvarez *et al.* 1979). The reduction in organic matter associated with fire may also facilitate contact between the roots and the ectomycorrhizal fungi by reducing competition (Herr *et al.* 1994; Petersen 1970). This field study was conducted three years after the prescribed fires. These affects may have abated as the humus layer had several seasons to redevelop.

There was no significant correlation between fire intensity and ectomycorrhizal colonization of *P. resinosa* nor *P. strobus* in either study. Fire consumes organic matter

and total nitrogen and phosphorus decrease after fire whereas available nitrogen and phosphorus increase (Raison 1979). Ectomycorrhizae are more abundant in soils with relatively low amounts of available N and/or P (Allen 1991; Björkman 1949; Hacskaylo 1957; Hacskaylo and Snow 1959; Marx *et al.* 1977; Menge *et al.* 1977). Bioassays of the soil were not performed so the amount of available N and P was not determined.

Although it is not well documented in temperate forests, the loss of mineral nutrients is related to fire intensity (Evans and Allen 1971; Wein and Maclean 1983). Thus, it is speculated that ectomycorrhizal colonization increases with fire intensity and the accompanying volatilization of soil minerals. However, the absence of a significant correlation between fire intensity and both species in both studies may be due to time since the fire. The ectomycorrhizal fungi associated with *P. strobus* and *P. resinosa* may be particularly sensitive to the changes in the humus layer in this stand which was dominated by *P.banksiana* (Figure 7).

Although all of the greenhouse seedlings' roots were ectomycorrhizal, the eight week duration of the greenhouse study may not have been adequate for a significant relationship between fire intensity and colonization to become apparent. Usually seedlings are ectomycorrhizal by three months (Allen 1991). However, each species is different in their growth requirements and tolerances (Burns and Honkala 1990). For example, *P. strobus* commonly germinates and grows in partial shade (Burns and Honkala 1990) but there was no shade to relieve the seedlings in the greenhouse.

The curvilinear patterns observed in all four correlations may be due to various

site parameters and thresholds. The fires were done on different days with different weather conditions and soil moisture contents. Fire may cause an initial fungal flush which abates at intermediate intensities and then rises.

In general, fungal colonization after fire has been found to depend on pre-fire soil moisture content (Dunn *et al.* 1985). Heat acts as a catalyst in the denaturing process (Dunn *et al.* 1985). Therefore, an increase in soil moisture content results in a decrease of fungi with heating (Dunn *et al.* 1985). In previous studies, it has been hypothesized that fire reduces germination of ectomycorrhizal fungal propagules and/or mycelium (Petersen 1970; Wicklow and Hirschfield 1979; Carpenter *et al.* 1987). Because this study was performed three years after burning, the effects of the pre-fire moisture content will have abated.

Two months after the out-planting of the seedlings in their study, Herr *et al.* (1994), at PNFI, assessed both *P. strobus* and *P. resinosa* for ectomycorrhizal colonization in the same manner as this study. In comparison with their results, it appears that ectomycorrhizal colonization increased slightly over the two years for all of the treatments. An increase in colonization with stand age may be due to the reduction, over time, of the disturbance induced nutrient flush and the subsequent decrease of nutrient availability in the rooting zone. With fewer resources, the seedlings may form greater numbers of feeder roots with higher ectomycorrhizal colonization to compete for the dwindling resources. Degree of ectomycorrhizal infection tends to be highest when plants are grown in soils with moderately low or unbalanced nutrient status (Vogt *et al.* 1983). However, Vogt *et al.* (1983) found that mycorrhizal colonization was only

significantly different when stands of *Pseudotsuga menziesii* reached the ages of 45 and 46 years. The results of this study and Herr *et al.* (1994) may provide support for the hypothesis that after fire there is higher colonization with stand age (Vogt *et al.* 1983). However, the two years difference in seedling age, in this case, many not be sufficient to yield significant findings.

The significance of the higher level interactions for the field study and the greenhouse study can not easily be explained (Tables 4, 6, &7). Even within a controlled environment experiment, certain parameters can not be monitored. The attempt to account for confounding parameters in an ecological setting is an immense, and often unattainable task. Variations in the microsite can be affected by a plethora of factors ranging from biological to climatic. These factors not only remain unregulated but are not unaccounted for as experimental parameters. Thus, an explanation of the significant higher level interactions may be due to the large number of samples and the ecological setting of this experiment.

The effects of prescribed burning on ectomycorrhizal colonization are of particular importance because of the benefits of ectomycorrhizal symbiosis (Herr *et al.* 1994). A large number of these fungi act as pioneer species and play an important role in nutrient cycling and immobilization in fire-disturbed ecosystems (Carpenter and Trappe 1985; Carpenter *et al.* 1987). Preparation of a suitable seedbed/planting-bed after harvesting is a critical step in silviculture. In order to promote sustainability, it is important to understand natural forest processes. In Canada, where a great deal of forest regeneration and nutrient cycling is dependent on fire (Bonan and Shugart 1989; Van

Wagner 1990), prescribed burning is an effective component of silvicultural planning. Prescribed fire is ideal as it reduces growth inhibiting humus layers and increases the availability of soil nutrients. Silvicultural prescriptions, which include burning, promote sustainable and diverse ecosystems. The continuation of this study, and others like it, is required to provide a basis for educated silvicultural decisions and practices.

Chapter 3:

The effect of prescribed burning on vesicular-arbuscular mycorrhizal colonization of *Trifolium repens* and *Agrostis palustris* in a *Pinus banksiana* stand

Introduction

Fire is a fundamental and potent force in shaping the boreal and Great Lakes-St. Lawrence forest regions. Periodic wildfires and prescribed burning have many affects on soil microfauna and microflora (Ahlgren and Ahlgren 1965). Although the effects of fire have been examined in many different kinds of ecosystems (Ahlgren and Ahlgren 1960; Ahlgren 1976; Engstrom and Mann 1991; Kozlowski and Ahlgren 1974; Methven and Murray 1974), there remains a paucity of information on the effects of fire on soil fungal populations so far as VAM are concerned (Dunn *et al.* 1985). Perhaps the most time consuming and technically involved microfungi to examine are VAM.

VAM fungi are the least understood of the mycorrhizal fungi examined in association with fire. This may be due, in part, to the physical difficulties associated with the examination of VAM and to the fact that, typically, fire-driven forest ecosystems in Canada are mainly colonized by ectomycorrhizal fungi (Allen 1991). Nonetheless VAM fungi are recognized as being important contributors to herbaceous plant growth (St. John and Coleman 1983).

As severity of many disturbances increases, there is a loss of VAM propagules and a decrease in VAM colonization (Daft and Nicholson 1974; Janos 1980; Reeves *et al.* 1979). However, other relevant literature has shown that colonization increases, decreases, or remains constant after fire (Ahlgren and Ahlgren 1965; Dunn *et at.* 1985; Widden and Parkinson 1975; Wright and Bollen 1961). The effects of fire on VAM colonization is variable and may depend on pre-fire conditions (Dunn *et al.* 1985).

Colonization of roots by VAM after fire may depend on fire intensity, soil and litter moisture content, soil type, litter depth, season\time of year of burning (Dunn *et al.* 1985) and soil temperature (Klopatek *et al.* 1988). In general, steam heat kills a greater number of microbes than does dry heat (Baker 1970). However, in a pinyon-juniper woodland, plants grown in soil with dry pre-fire conditions had lower VAM colonization than in soil with wet pre-fire conditions (Klopatek *et al.* 1988). Klopatek *et al.* (1988) also observed a positive correlation between decreasing VAM colonization and increasing soil temperature. Regardless of pre-fire conditions, there is a decrease in viable propagule densities with fire (Vilarino and Arines 1991). Several researchers have observed that burning tends to reduce the VAM infectivity of soil (Dhillion *et al.* 1988; Gibson and Hetrick 1988; Klopatek *et al.* 1988; Vilarino and Arines 1991).

In the boreal and Great Lakes-St. Lawrence forest regions, the plant species colonized by VAM provide competition for Canada's major crop species. In order to use fire as an effective silvicultural tool, it is important to understand the effects of fire at each ecological level. The objective of this study was to examine the relationship between fire intensity and pre-fire fine fuel moisture content and VAM colonization of

Trifolium repens (white clover) and *Agrostis palustris* (creeping bentgrass) in a standing jack pine (*P. banksiana*) stand.

Methods and Materials

Study site

The same study area was used as described in Chapter 2.

Vesicular-arbuscular mycorrhizae (VAM) assessment

Soil from the three metre by three metre standing timber plots was used. Two soil cores from thirty-one burns and four non-burns were sown with ten *Agrostis palustris* seeds and ten *Trifolium repens* seeds respectively on June 3, 1994. The soil cores were 20 centimetres in diameter and were placed in 15 centimetre diameter plastic pots. *A. palustris* and *T. repens* were used as bait species because they are both common species that are known to be VAM (Table 1). The plants were grown for 75 days and were harvested on August 10, 1994.

The roots from each pot were cleared with a 5 percent potassium hydroxide solution (Brundrett *et al.* 1993). Specimens were autoclaved for eight minutes at 121 degrees Celsius on slow exhaust cycle. Roots were then rinsed in distilled water and stained with a 0.03 percent (w\v) chlorazol black E (CBE) solution (Brundrett *et al.* 1984). The roots were heated in the CBE solution at 90 degrees Celsius for one hour and then drained (Brundett *et al.* 1993; Brundett *et al.* 1984). The roots were stored in a 25 percent glycerol solution until assessed.

The roots were assessed for VAM according to the magnified intersections

method (McGonigle *et al.* 1990). Roots were mounted in glycerin on microscope slides and covered with 40 by 22 millimetre coverslips. Five slides were used for each subsample, but all slides for a subsample were treated as a single unit, and not as sub-subsamples (McGonigle *et al.* 1990). However, in cases where there were not enough roots, a minimum of three and a half slides were used. Roots were aligned parallel to the long axis of the slides and observed at magnification x200 with a Zeiss Universal microscope. The field of view of the microscope was moved with the mechanical stage graticule to make passes across each slide perpendicular to its long axis and the roots (McGonigle *et al.* 1990). This was done until 150 intersections for each slide were examined. All intersections between roots and the vertical eyepiece crosshair were considered except where the cortex was missing or severely damaged (McGonigle *et al.* 1990).

The plane of focus was moved through the entire root and a note was made of whether the vertical crosshair intersected any arbuscules or not (McGonigle *et al.* 1990). Colonization was quantified as proportion of arbuscules divided by total number of intersections examined.

Statistical Analyses

All data were transformed. With log(x+1) transformation, where x is percent VAM colonization, the data had the lowest variance and a symmetric distribution. t-tests were used to determine the difference in colonization between the two species. Correlation of VAM formation with fire intensity and pre-fire fine fuel moisture content was investigated by determining Spearman's correlation matrix. The alpha level for

rejecting the null hypothesis was set at α=0.01 due to the extensive testing, the large sample size and to attempt to avoid a Type I error. All analyses were conducted using SPSS 6.1 (1994).

Results

VAM root colonization of *T. repens* had a mean of 1.4 percent which was significantly lower than that found in *A. palustris* with a mean of 17 percent. Neither *T. repens* nor *A. palustris* correlated with either fire intensity or moisture content (Figures 10, 11, 12, and 13).

The majority of both the *A. palustris* and *T. repens* seeds planted on non-burned substrate failed to germinate. Those seeds planted on the non-burned substrate which did grow into plants were poorly established and lacked sufficient roots for analysis.

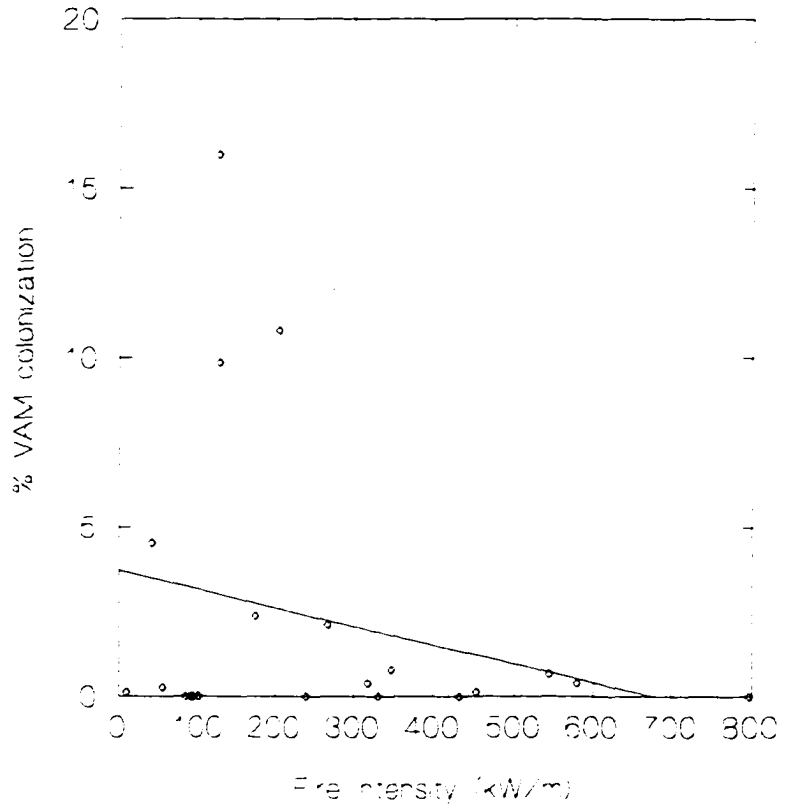


Figure 10. The relationship between fire intensity and percent vesicular-arbuscular mycorrhizal colonization in *T. repens*. The correlation between % VAM colonization and fire intensity is not significantly different from zero.

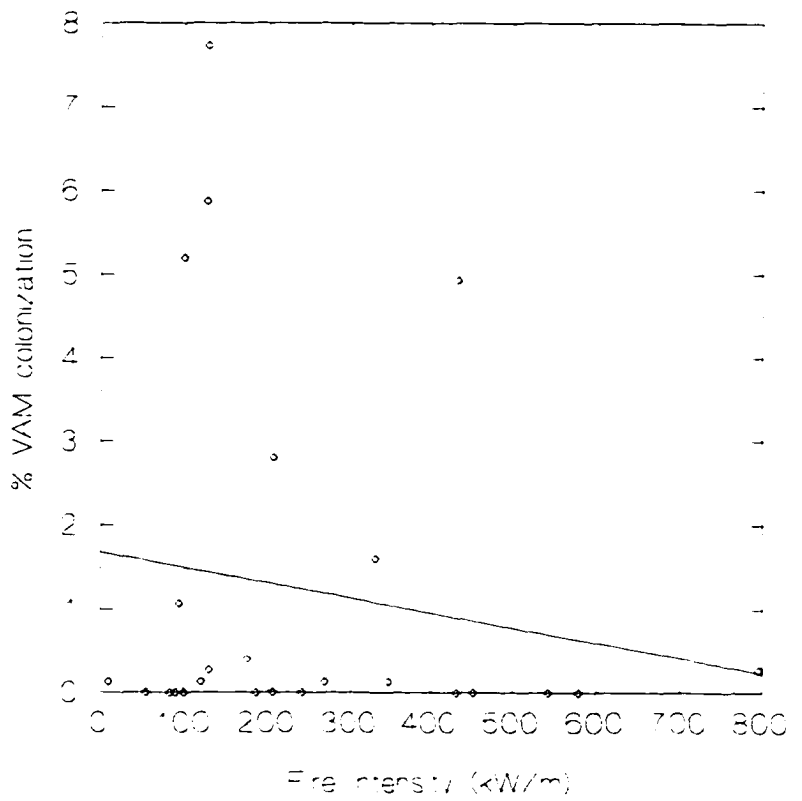


Figure 11. The relationship between fire intensity and percent vesicular-arbuscular mycorrhizal colonization in *A. palustris*. The correlation between % VAM colonization and fire intensity is not significantly different from zero.

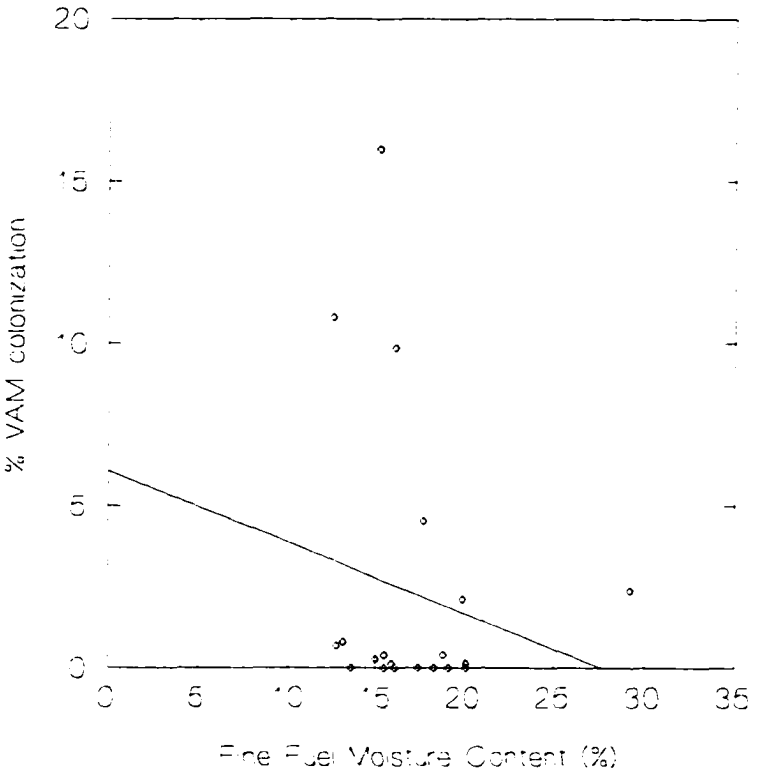


Figure 12. The relationship between prefire fine fuel moisture content and percent vesicular-arbuscular mycorrhizal colonization in *T. repens*. The correlation between % VAM colonization and fine fuel moisture content is not significantly different from zero.

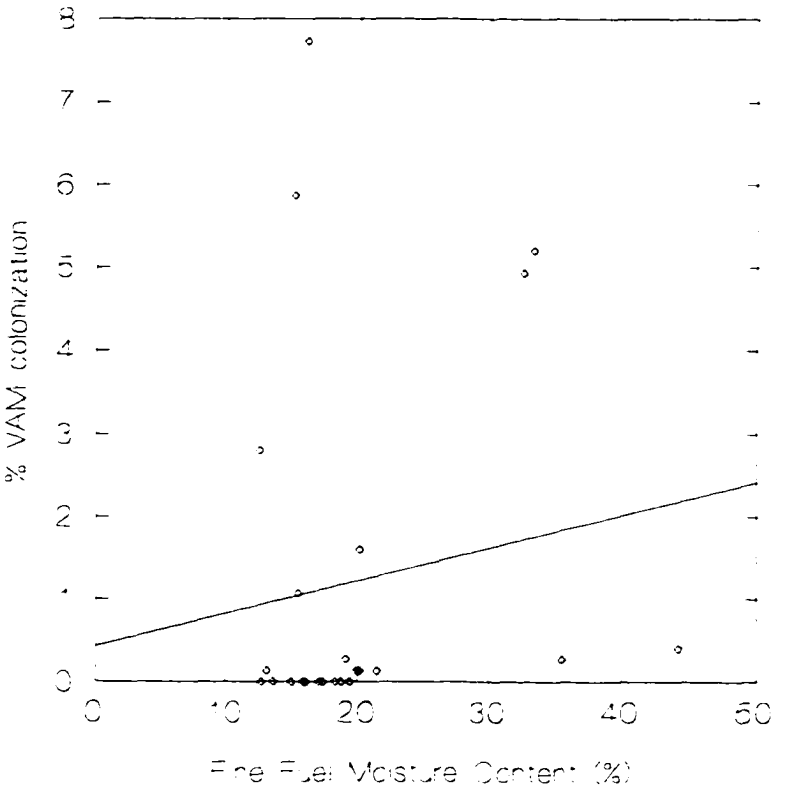


Figure 13. The relationship between prefire fine fuel moisture content and percent vesicular-arbuscular mycorrhizal colonization in *A. palustris*. The correlation between % VAM colonization and fine fuel moisture content is not significantly different from zero.

Discussion

Since many of the Frontier Lake experimental plot understorey species are VAM (Table 1), colonization of *T. repens* and *A. palustris* by VAM fungi was expected. The lack of growth and seed germination failure on the non-burned substrate may indicate that these species do not germinate in the presence of profuse organic matter, and do indeed require fire or duff removing disturbance to germinate. As is the case with early stage colonizers, *T. repens* and *A. palustris* are shade intolerant. Studies have found that VAM colonization and propagules are greater on non-burned substrate (Allsopp and Stock 1994; Dhillion *et al.* 1988; Klopatek *et al.* 1988). It can be speculated that the seeds on the non-burned plots would germinate with a reduction in organic matter, and that these plants would have higher colonization than the plants grown on the burned substrate. However, this study was executed one year subsequent to burning; there may now be no significant decrease in colonization as they may have risen to their pre-fire levels (Allsopp and Stock 1994; Dhillion *et al.* 1988).

Since the severity of disturbance has been seen to correlate with a reduction in VAM colonization (Daft and Nicholson 1974; Janos 1980; Reeves *et al.* 1979), it can also be speculated that had the plants been on site prior to burning, and thus been permitted to repopulate vegetatively, the plants on the non-burned substrate would have greater colonization compared to those of the burned substrate.

Although colonization has been observed to decrease with increasing temperature (Klopatek *et al.* 1988), there was no relationship with fire intensity for either species. The fire intensities in this study may have been so high as to not show a relationship. However, it is likely that in this ecosystem type, fire has deleterious affects on VAM colonization.

The *T. repens* and *A. palustris* were planted on soils which had been burned the previous year. It has been found that the initial increase in VAM colonization decreases with time since the fire (Bentivenga and Hetrick 1991). However, this has been reported in a tallgrass prairie ecosystem where the dominant species are VAM, unlike *P. banksiana* stands where the dominant species are colonized by ectomycorrhizae (Allen 1991).

In the boreal and Great Lakes-St. Lawrence the species colonized by VAM provide competition for Canada's major crop species. In order to use fire as an effective silvicultural tool it is important to understand the effects of fire at each ecological level. The ultimate goal is to use research such as this in context with silvicultural planning and to find, for each stand/forest, an optimum set of fire intensities to promote crop species growth and inhibit that of the competition. VAM colonization is dependent on several factors. Additional research is required to better understand the dynamics of fungi in non-burned soils.

Chapter 4:

The effect of fire intensity on soil fungi carpophore production

Introduction

In many of Canada's temperate forests, fire is a natural recurrent disturbance that dramatically influences short- and long-term forest dynamics. A major group of organisms affected by fire are the forest fungi in the Ascomycotina and Basidiomycotina sub-divisions. Fire undoubtedly influences the species richness and assemblages of these macrofungi. Burning can predispose a site to infection of certain fungi such as *Rhizina undulata*. Under natural conditions, phoenicoid, or fireplace fungi, have thus far been found exclusively on heat treated substrates including burned forest ground (Petersen 1970), soil heated by steam (Warcup 1990), and fresh volcanic tephra mixed with organic material (Carpenter *et al.* 1987). There are several documentations of unique fungi appearing on site following a fire (Warcup 1990; Carpenter *et al.* 1987; Widden and Parkinson 1975).

New ectomycorrhizal fungal species, such as *Muciturbo reticulatus*, appeared in a eucalypt forest in South Australia (Warcup 1990). New ectomycorrhizal fungi were also observed in the Mount St. Helens volcano devastation zone (Carpenter *et al.* 1987). Fungal species were found on the volcanic tephra which habitually appear after prairie or forest fires (Carpenter *et al.* 1987). Although many phoenicoid fungi do not interfere

with tree growth, some are pathogenic. In a *Pinus contorta* stand in Alberta, fire was observed to promote favourable growth conditions for the pathogen *Cylindrocarpon destructans* (Widden and Parkinson 1975).

There are two main hypotheses explaining selective fungal colonization after fire. Fungi such as *Rhizina undulata* and *Anthracobia melaloma* may depend on the heat generated during a fire, termed the heat pulse, to stimulate ascospore germination (Carpenter *et al.* 1987; Petersen 1970; Wicklow 1975). After fire the most numerous of the fungi are from the sub-division Ascomycotina because the ascospores tend to be more resistant to environmental factors than the conidia of the Fungi Imperfecti (Widden and Parkinson 1975). The second hypothesis speculates that fire may reduce competition thus enabling carbonicolous fungi to pioneer (Carpenter and Trappe 1985; Wicklow and Hirschfield 1979). Wicklow and Hirschfield (1979) thought that early soil colonists exhibit a low tolerance to other soil microorganism and would, therefore, be short-lived. These fungi would presumably not grow on site prior to the next natural fire (Wicklow and Hirschfield 1979).

The purpose of this study was to provide the rudimentary information for an intensive examination of the effects of fire on fruiting of mycorrhizal and other macrofungi. The objective of this study was to determine the effects of fire on fungal carpophore production in a *P. banksiana* stand.

Methods and Materials

Study site and carpophore production analyses

The study area is described in Chapter 2.

The 31 three metre by three metre burned plots and nine non-burned plots, as described in McAlpine (1995) and Herr *et al.* (1994), were examined between June 13 and October 18, 1994. The plots were surveyed weekly for fungal fruiting bodies. All of the mushrooms that formed each week were removed from the site for identification. Identification of the fungi was verified by Agriculture Canada in Ottawa (Redhead pers. comm.; Dalpe pers. comm.)

Results

Sixteen fungal specimens were identified to species, fourteen to genus, and seven unidentified specimens (Species 1-7) that were different from the other 30 specimens were present (Table 9). Thirty-one fungi types were found on the burned plots, nine were found on the non-burned plots, and seven were found on both the non-burned plots and the burned plots.

In June *Aleuria aurantia*, *Laccaria laccata*, *Pholiota* spp., and *Xermaphalina cornuii* were present. *A. aurantia* was observed up until September while the latter three species were found up until October 18. Species 2, *Cantharellus cibarius*, *Mycena* sp., *Russula* spp., *Rhizina undulata*, and *Tylopilus felleus* were found in July: *C. cibarius*, *Rhizina undulata*, and *T. felleus* were also found in August, the *Mycena* sp. was present in September, and the *Russula* spp. were present up to the completion of the sampling in October. Species 5, *Suillus pictus*, and *Lyophyllum* sp. appeared in August. The *Lyophyllum* sp. was also observed in September. Species 6 and 7, *Clavicorona pyxidata*, *Coltricia* sp., *Cortinarius* sp., *Lycoperdon perlatum*, *Dermocybe* sp., *Inocybe* sp., *Psathyrella* sp., *Pholiota highlandensis*, *and Lactarius vinaceorufescens* appeared in September. *Cortinarius* sp., *Inocybe* sp., *Psathyrella* sp., *Pholiota highlandensis*, and *Lycoperdon perlatum* were also present in October. An *Armillaria* sp. appeared in October along with *Clavulinopsis fusiformis*, *Cystoderma*

amianthium, *Suillus americanus*, *Gymnopolis* sp., *Rickenella fibula*, and Species 1, 2, 3, and 4. The number of fungal groups appeared to increase with time (Figure 14).

Several species occurred only on the burned sites. These were *A. aurantia*, *S. pictus*, *C. pyxidata*, *L. perlatum*, *R. undulata*, *Mycena*, *L. vinaceorufescens*, *Armillaria* sp., *C. amianthium*, *Lyophyllum* sp., *Gymnopilus* sp., *S. americanus*, *R. fibula*, *C. fusiformis*, *Coltricia* sp., *Inocybe* sp., *Psathyrella* sp., and Species 1-7. *C. cibarius* and the *Dermocybe* sp. were the only species to occur exclusively on the non-burned sites.

Table 9. Fungal species found on the burned and non-burned plots at the Frontier Lake Experimental Site.

Fungal Species	Non-burned Plots	Burned Plots	Mycorrhizal (M) Saprophytic (S) or Pathogenic (P)[1]
Aleuria aurantia (Fr.) Fuckel[2]		✓	P
Amanita porhyria (A. & S.: Fr.) Secr.	✓	✓	M
Armillaria (1 species)[2]		✓	P
Cantharellus cibarius Fr.	✓		M
Clavicorona pyxidata (Pers.: Fr.) Doty		✓	S
Clavulinopsis fusiformis(Sow.: Fr.) Corner		✓	S
Coltricia (1 species)[2]		✓	S
Cortinarius (2 species)	✓	✓	M
Cystoderma[2] *amianthium*		✓	
Dermocybe (1 species)	✓		M
Gymnopilus[2](1 species)		✓	
Inocybe (1 species)		✓	M
Laccaria laccata[2](Scop.: Fr.) Cke	✓	✓	M
Lactarius vinaceorufescens Smith		✓	M
Lycoperdon[2]*perlatum* Pers.		✓	S
Lyophyllum (2 species)		✓	
Mycena[2](1 species)		✓	S
Pholiota[2] *highlandensis* (Pk. Smith & Hesler) (+ 1 species)	✓	✓	S

Table 9 continued.

Fungi Species	non-burned plots	burned plots	Mycorrhizal(M) Saprophytic (S) or Pathogenetic (P)
Psathyrella[2] (1 species)		✓	S
Rickenella[2] *fibula* (Bull.: Fr.) Raith		✓	S
Rhizina undulata[2]		✓	P
Russula (3 species)	✓	✓	M
Suillus americanus (Pk.) Snell: Slipp & Snell		✓	M
Suillus pictus (Pk.) Smith & Thiers		✓	M
Tylopilus fellius (Bull.: Fr.)	✓	✓	M
Xeromphalina cornuii	✓	✓	S
Species 1-7		✓	

[1]Fungi were categorized using Pera and Alvarez 1995; Treu and Miller 1993; and Waller and Agerer 1993.

[2]Fungi found on burned over areas in the literature (all are not necessarily phoenicoid)(Petersen 1970; Phillips 1991; Carpenter *et al.* 1987).

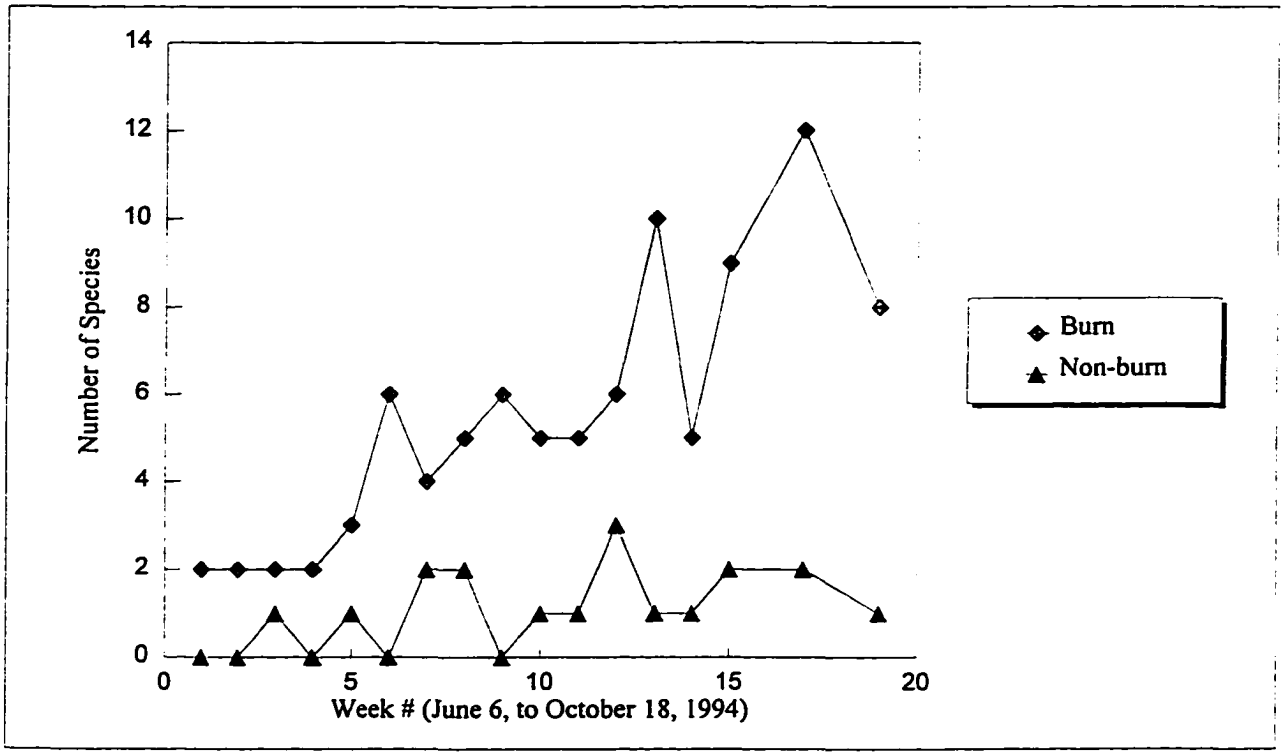


Figure 14. Seasonal variation in number of fungal species fruiting on the burned and non-burned plots at the Frontier Lake Experimental Site.

Discussion

Many of the fungi present on both the burned plots and non-burned plots are mycorrhizal (Table 9). These fungi benefit trees via enhanced growth, health, and root resistance to pathogens (Allen 1991; Mikola 1973; Petersen 1970). For example, species from the genus *Amanita* have been observed to naturally detoxify mine spoils for cadmium in a *P. resinosa* stand (Medve and Sayre 1994). Another well known ectomycorrhizal phoenicoid fungus, found in this study, was *L. laccata*. *L. laccata* has been observed to suppress the root pathogen *Fusarium oxysporum* and promote growth in *Pseudostuga menzesii* seedlings (Sinclair *et al.* 1982). Fire, even at low intensities, stimulates the growth of these beneficial fungi. However, the growth of potentially pathogenic fungi in the genera *Pholiota*, *Armillaria*, and *Mycena* are also stimulated by fire (Jung *et al.* 1992). For example, the root pathogen, *Rhizina undulata*, was credited with seedling mortality after a lightning fire in a *P. patula* plantation in the south eastern Transvaal, South Africa (Lundquist 1993). Saprophytic fungi are expected on a burned site due to the dead wood and debris associated with the fire. These fungi are not competitors with mycorrhizal fungi since they rely on different resources.

Phoenicoid fungi, such as some *Psathyrella* species, occur exclusively on the burned plots, but, some fungal species may occur on both the burned and non-burned plots due to the vegetation mosaic left by the fire (Hansen *et al.* 1991). Fire burns an

area heterogeneously and therefore increases species diversity over the stand (Hansen *et al.* 1991). Often there are species which fail to grow after fire. For example, species such as *C. cibarius* may not appear because of soil moisture loss (Grochowski and Ostalski 1993). Thus the fungi found on the burned site are not all necessarily phoenicoid but are disturbance originating species such as *A. aurantia* (Petersen 1970).

Although the number of fungi found on the burn and the non-burn sites was different, the seasonal variation in fungal numbers was similar (Figure 14). The mosaic left by the fire will encourage the growth of a larger array of fungi (Hansen *et al.* 1991) than the forest floor of the non-burned sites. This pattern, where there is an increase in fruitification and number of fungi in late summer and fall is supported by Petersen's 1970 study.

Another unique pattern in colonization after fire is characterized, over several years, by early colonization by certain discomycetes and pyrenomycetes (Ascomycotina) followed by secondary colonization of basidiomycetes and other ascomycetes (Bartoli *et al.* 1991; Carpenter *et al.* 1987; Petersen 1970). Because there was only one season of sampling since the fire, no such pattern was discerned in this study. However, because of the nature of this study an exhaustive species list is unattainable; therefore some species may have gone uncollected (Redhead pers. comm.). Nonetheless many of the same species found by Carpenter *et al.* (1987) one to three years subsequent to the eruption of Mount St. Helens, are of the same genus and/or species observed in this study; *R. undulata*, *Pholiota carbonaria*, *Psathyrella carbonicola*, *Aleuria aurantia*, *Psathyrella* sp., and *Rickenella* sp. were found by

Carpenter *et al.* (1987).

There tends to be a distinct pattern of succession of ectomycorrhizal fungi according to plant age (Shaw *et al.* 1992). For example, *Cortinarius* species are observed to be late-stage mycorrhizal fungi under *P. sylvestris* (Shaw *et al.* 1992). However, the literature is scant with respect to *P. banksiana* stands and fungal succession.

Many of the mycorrhizal fungi show host specificity (Browning and Whitney 1992; Kendrick 1985; Martinez-Amores *et al.* 1990/1991). Fungi benefit some trees more than others but are rarely observed to grow exclusively with one tree species (Molina and Trappe 1982). For example, *P. patula* and *P. radiata* had better growth with *L. perlatum* than with *R. brevipes* (Marinez-Amores *et al.* 1990/1991). Molina and Trappe (1982) found that *Suillus brevipes* grew best and almost exclusively with *Pinus* species. Since the forest at the Frontier Lake study site is comprised of *P. resinosa*, *P. banksiana*, and *P. strobus*, it can be assumed that *S. brevipes* formed ectomycorrhizal associations with all three tree species.

Further studies should be done distinguishing fungi grown at different fire intensities. Studies of such calibre may allow for the manipulation of the forest floor to yield beneficial mycorrhizal fungi. The promotion of these fungi would result in increased tree and stand health which would bring the forestry industry closer to the goal of sustainability.

Chapter 5:

Conclusion

One goal in fire ecology research is to use studies such as this in context with silvicultural planning, and to find for each stand/forest, an optimum set of fire intensities to promote crop species growth and inhibit that of the competition. The ideal intensity would result in: a) an increase in ectomycorrhizal colonization which in turn would enhance the health of the crop species; and b) a decrease in VAM colonization thus decreasing the overall health of the competition (Herr *et al.* 1994).

In this study each *Pinus* species had different levels of ectomycorrhizal colonization of which both increased slightly with fire. Studies have found that increased mycorrhiae colonization was accompanied by an increase in seedling survival and health (Herr *et al.* 1994). Therefore, fire as a silvicultural tool, indirectly, increases crop health, resilience, and survival.

Neither *T. repens* nor *A. palustris* VAM colonization correlated strongly with fire intensity. They had very low average colonization, and it can therefore be hypothesised that there would be greater colonization in plants in an area that was not burned and that fire, of any intensity, impedes VAM colonization (Allsopp and Stock 1994; Dhillion et al. 1988; Klopatek *et al.* 1988). Since it has been one year since the fire, the VAM colonization rate may be increasing and these values may be higher than

those found at the end of the last season. The next step in VAM research is to determine how fire affects VAM colonization over time. It is important to note if colonization exceeds that of pre-fire VAM over an extended period of time.

Eleven fungal species surveyed in this study are known to be mycorrhizal, nine are saprophytic, and two are pathogenic (Table 9). All of the saprophytic and pathogenic fungal species occurred on the burned plots. In future studies it is important to quantify and compare the potentially negative growth and survival effects of these fungi to the effects of the mycorrhizal fungi.

Research into the aforesaid areas, along with assessment of pre-fire conditions affecting soil dynamics, may provide stronger reasons for using prescribed fire as a silvicultural tool. Future forestry studies need to compare the ecological dynamics following wildfire and prescribed fire with an emphasis on the factors affecting crop tree health. In conducting research such as this, a stronger basis is provided to manage the Canadian temperate and boreal forests in a manner that emulates natural disturbance caused by fire.

A new forest resource management paradigm is evolving. This new standard encompasses decisions based on sustainability, species diversity, habitat protection, and natural regeneration and emphasises alternative methods of harvesting, site preparation, and regeneration (Anonymous 1995; Perrin 1993). Prescribed fire is site specific. It is also a costly and dangerous endeavour. Therefore, it is imperative that fire be an ecologically safe and sound alternative and that it be suited for the ecosystem/stand for which it is intended. Studies such as this one contribute by adding to the knowledge

base for these crucial silvicultural decisions.

Literature Cited

Acea, M.J. and T. Carballas. 1990. Principal components analysis of the soil microbial population of humid zone of Galicia (Spain). Soil Biol. Biochem. 22: 749-759.

Adedeji, F.O. 1983. Effect of fire on soil microbial activity in Nigerian southern Guinea savanna. Rev. Ecol. Biol. Sol. 20: 483-492.

Ahlgren, C.E. 1976. Regeneration of red pine and white pine following wildfire and logging in northeastern Minnesota. J. For. 135-140.

Ahlgren, I.F. and C.E. Ahlgren. 1960. Ecological effects of forest fires. Bot. Rev. 26: 483-533.

Ahlgren, I.F., and C.F. Ahlgren. 1965. Effects of prescribed burning on soil microorganisms in a Minnesota jack pine forest. Ecology 46: 304-310.

Alexander, M.E. 1982. Calculating and interpreting forest fire intensities. Can. J. Bot. 60: 349-357.

Allen, M. F. 1991. The ecology of mycorrhizae. Cambridge studies in ecology. Cambridge University Press. Great Britain. 184 pp.

Allsopp, N. and W.D. Stock. 1994. VA mycorrhizal infection in relation to edaphic characteristics and disturbance regime in three lowland plant communities in the south-western Cape, South Africa. J. Ecol. 82: 271-279.

Alvarez, I.F., D.L. Rowney, and F.W. Cobb, Jr. 1979. Mycorrhizae and growth of white fir seedlings in mineral soil with and without organic layers in a California forest. Can. J. For. Res. 9: 311-315.

Amaranthus, M.P., and J.M. Trappe. 1993. Effects of erosion on ecto- and VA mycorrhizal inoculum potential of soil following forest fire in southwest Oregon. Plant and Soil 150: 41-49.

Anderson, V.L. 1970. Restriction errors for linear models (an aid to develop models for designed experiments. Biometrics 26: 255-268.

Anonymous. 1987. Canadian Forest Fire Danger Rating System: User's guide. Canadian Forestry Service Fire Danger Group, three ring binder (unnumbered publication), For. Can., Hull, PQ.

Anonymous. 1995. Forest practices code of British Columbia: Biodiversity guidebook. Province of British Columbia. BC Environment. ISBN 0-7726-2619-7.

Arianoutsou-Faraggitaki, M. and N.S. Margaris. 1982. Decomposers and the fire cycle in a phryganic (East Mediterranean) ecosystem. Microb. Ecol. 8: 91-98.

Atlas, R.M. and R. Bartha. 1981. Microbial Ecology: Fundamentals and applications. 3rd ed. The Benjamin/Cummings publishing company, Inc. Redwood City, CA. 563 pp.

Baar, J., F. W. de Vries, and T. W. Kuyper. 1993. Inhibition of the ectomycorrhizal inoculum potential by litter and humus in Scots pine forests pp. 7-12 *in* Larry Peterson and Michelle Schelkle (eds.) Abstracts of Oral and Poster Presentations of the 9th North American Conference on Mycorrhizae. University of Guelph.

Baar, J. and T.W. Kuyper. 1993. Litter removal in forests and effect on mycorrhizal fungi pp. 275-286 *in* D.N. Pegler, L. Boddy, B. Ing, and P.M. Kirk, (eds.) Fungi of Europe: Investigation, recording, and conservation. Kew: Royal Botanic Gardens.

Baker, K.F. 1970. Selective killing of soil microorganisms by aerated steam pp. 234-239 *in* T.A. Toussoun, R.V. Bega, and P.E. Nelson (eds.) Root diseases and soil-borne pathogens. University of California Press.

Bartoli, A., R. Gerdol, and G. Massari. 1991. Soil fungi succession in a Mediterranean "macchia" after fire. Rev. Ecol. Biol. Sol. 28: 387-402.

Bentivenga, S.P. and B.A.D. Hetrick. 1991. Relationship between mycorrhizal activity, burning, and plant productivity in tallgrass prairie. Can. J. Bot. 69: 2597-2602.

Bisset, J. and D. Parkinson. 1980. Long-term effects of fire on the composition and activity of the soil microflora of a subalpine, coniferous forest. Can. J. Bot. 58: 1704-1721.

Björkman, E. 1949. The ecological significance of the ectotropic mycorrhizal associations in forest trees. Sven. Bot. Tidskr. 43: 223-262.

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. 19th An. Rev. Ecol. Sys. 20: 1-28.

Browning, M.H.R. and R.D. Whitney. 1993. Infection of containerized jack pine and black spruce by *Laccaria* species and *Thelephora terrestris* and seedling survival and growth after out-planting. Can. J. For. Res. 23:330-333.

Brundrett, M., G. Murase, and B. Kendrick. 1990. Comparative anatomy of roots and mycorrhizae of common Ontario trees. Can. J. Bot. 68: 551-578.

Brundrett, M. L. Peterson, L. Melville, H. Addy, T. McGonigle, and G. Schaffer. 1993 unpubl. Anatomy workshop handbook. Ninth North American conference on Mycorrhizae. University of Guelph. Guelph, Ontario. Aug. 8-12. 154 pp.

Brundrett, M.C., Y. Piche, and R.L. Peterson. 1984. A new method for observing the morphology of vesicular-arbuscular mycorrhizae. Can. J. Bot. 62: 2128-2134.

Buckman, R.E. 1964. Effects of prescribed burning on hazel in Minnesota. Ecology 45: 626-629.

Burgess, D.M., and I.R. Methven. 1977. The historical interaction of fire, logging, and pine: a case study at Chalk River, Ont. Can. For. Ser., Information report PS-X-66.

Burns, R.M. and B.H. Honkala. 1990. Silvics of North America. Washington, D.C.: U.S. Department of Agriculture. Forest Services. Agr. Hnbk. 654.

Buscot, F. 1989.Field observations on growth and development of *Morchella rotunda* and *Mitrophora semilibera* in relation to forest temperature. Can. J. Bot. 67: 589-593.

Byram, G.M. 1959. Combustion of forest fuels pp. 61-89 *in* K.P. Davis, (ed.) Forest fire: control and use. McGraw-Hill Book Co., N. Y.

Callan, B.E. 1993. Rhizina root rot of conifers. Forest pest leaflet. Nat. Res. Can. No. Fo 29-6/56-1993E. Victoria, B.C. 5 pp.

Carpenter, S.E. and J.M. Trappe. 1985. Phoenicoid fungi: a proposed term for fungi that fruit after heat treatment of substrates. Mycotaxon 22: 203-206.

Carpenter, S.E., J.M. Trappe, and J. Ammirati, Jr. 1987. Observations of fungal succession in the Mount St. Helens devastation zone, 1980-1983. Can. J. Bot. 65: 716-728.

Creasey, K.R. and T.R. Myland. 1993. Guidelines for seed pretreatment. Forest Resources Group Nursery and Seed Section. OMNR. 45 pp.

Cwynar, L.C. 1977. The recent fire history of Barron Township, Algonquin Park. Can. J. Bot. 55: 1524-1538.

Daft, M.J., and T.H. Nicholson. 1974. Arbuscular mycorrhizas in plants colonizing coal wastes in Scotland. New Phytol. 73: 1129-1138.

Danielson, R.M. 1984a. Ectomycorrhizal associations in jack pine stands in northeastern Alberta. Can. J. Bot. 62: 932-939.

Danielson, R.M. 1984b. Ectomycorrhiza formation by the operculate discomycete *Sphaerosporella brunnea* (Pezizales). Mycology 76: 454-461.

Deka, H.K., and R.R. Mishra. 1983. The effect of slash burning on soil microflora. Plant and Soil 73: 167-175.

De Vries, B.W.L., E. Jansen, H.F. Van Dobben, and Th.W. Kuyper. 1995. Partial restoration of fungal and plant species diversity by removal of litter and humus layers in stands of Scots pine in the Netherlands. Biodiv. Cons. 4: 156-164.

Dhillion, S.S., R.C. Anderson, and A.E. Liberta. 1988. Effect of fire on the mycorrhizal ecology of little bluestem (*Schizarium scoparium*). Can. J. Bot. 66: 706-713.

Diaz-Ravina, M., M.J. Acea, and T. Carballas. 1993a. Seasonal fluctuations in microbial populations and available nutrients in forest soils. Biol. Fertil. Soils 16: 205-210.

Diaz-Ravina, M., M.J. Acea, and T. Carballas. 1993b. Microbial biomass and C and N mineralization in forest soils. Biores. Tech. 43: 161-167.

Duchesne, L.C. and K.A. Rigal. 1995. Le feu et les microorganismes du sol. pp. 179-195 *in* J. A. Fortin, C. Charest, and Y. Piche (eds.) La symbiose mycorhizienne. Etat des connaissances. Orbis Publishers, Freligshburg, Quebec.

Duchesne, L.C., and M. Weber. 1993. High incidence of the edible morel *Morchella conica* in a jack pine, *Pinus banksiana*, forest following prescribed burning. Can. Field Nat. 107: 114-116.

Dunn, P.H., S.C. Barro, and M. Poth. 1985. Soil moisture affects survival of microorganisms in heated Chaparral soil. Soil Biol. Biochem. 17: 143-148.

Ek, M., P.O. Ljungquist, and E. Stenstrom. 1983. Indole-3-acetic acid production by mycorrhizal fungi determined by gas chromatography-mass spectrometry. New Phytol. 94: 401-407.

Engstrom, F.B., and D.H. Mann. 1991. Fire ecology of red pine (*Pinus resinosa*) in northern Vermont, U.S.A. Can. J. For. Res. 21: 882-889.

Evans, C.C. and S.E. Allen. 1971. Nutrient losses in smoke produced during heather burning. Oikos 22: 149-154.

Feller, M.C. 1982. Soil and other considerations in slashburning *in* T. Vold (ed.) Proceedings of the B.C. Soil Survey Workshop on Soil Interpretation in Forestry. APD Technical paper interpretation for Forestry No. 6, B.C. Ministry of Forests.

Frissell, S.S. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. Quat. Res. 3: 397-407.

Gibson, D.J., and B.A.D. Hetrick. 1988. Topographic and fire effects on the composition and abundance of VA-mycorrhizal fungi in tallgrass prairie. Mycologia 80: 433-441.

Grochowski, W. and R. Ostalski. 1993. Changes in the forest environment under a 65-year-old pine stand caused by sprinkling the forest ground. Instytutu Badawczego Lesnictwa. 769: 145-160.

Hacskaylo, E. 1957. Mycorrhiza of trees with special emphasis on physiology of ectotrophic types. Ohio J. Sci. 57: 350-357.

Hacskaylo, E., and A.G. Snow. 1959. Relation of soil nutrients and light to prevalence of mycorrhizae. U.S. Dep. Agric. For. Serv., Northeast For. Exp. Stn. Pap. No. 125.

Hansen, A.J., T.S. Spies, F.J. Swanson, and J.L. Ohmann. 1991. Conserving biodiversity in managed forests: Lessons from natural forests. BioSci. 41: 382-392.

Harley, J.L. and S.E. Smith. 1983. Mycorrhizal symbiosis. Academic Press, NY. 483 pp.

Harvey, A.E., M.J. Larsen, and M.F. Jurgensen. 1979. Ecology of ectomycorrhizae in northern rocky mountain forests pp. 12-27 *in* Environmental consequences of timber harvesting in rocky mountain coniferous forests. USDA For. Ser. Gen. Tech. Rep. INT-90.

Harvey, A.E., M.F. Jurgensen, and M.J. Larsen. 1980. Clearcut harvesting and ectomycorrhizae: survival of activity on residual roots and influence on a bordering forest stand in western Montana. Can. J. For. Res. 10: 300-303.

Heinselman, M.L. 1981. Fire succession in the conifer forests of Northern North America pp. 374-405 *in* D.C. West, H.H. Shugart, and D.B. Botkin (eds.) Forest succession, concepts and applications. Springer-Verlag, NY.

Hendrickson, O., and J.B. Robinson. 1982. The microbiology of forest soils a literature review. PNFI. Can. For. Ser. Information report PI-X-19.

Herr, D.G., L.C. Duchesne, R. Tellier, R.S. McAlpine, and R.L. Peterson. 1994. Effect of prescribed burning on the ectomycorrhizal infectivity of a forest soil. Int. J. Wildland Fire 4: 95-102.

Jalaluddin, M. 1969. Short communication: Micro-organic colonization of forest soil after burning. Plant and Soil 30: 150-152.

Janos, D. 1980. Mycorrhizae influence tropical succession. Biotropica 12: 56-64.

Johansson, M. 1994. Quantification of mycorrhizal infection in roots of *Calluna vulgaris* (L.) Hull from Danish Heathland. Soil Biol. Biochem. 26: 763-766.

Jones, J.R., and N.V. DeByle. 1985. Fire pp. 24-43 *in* N.V. DeByle and R.P. Winokur (eds.) Aspen: ecology and management in the Western United States. USDA For. Serv. Gen. Tech. Rep.

Jorgensen, J.R. and C.S. Hodges, Jr. 1970. Microbial characteristics of a forest soil after twenty years of prescribed burning. Mycologia. 62: 721-726.

Jorgensen, J.R. and C.G. Wells. 1971. Apparent nitrogen fixation in soil influenced by prescribed burning. Soil Sci. Soc. Amer. Proc. 35: 806-810.

Jung, H.G., F.R. Valdez, A.R. Abad, R.A. Blanchette, and R.D. Hatfield. 1992. Effect of white rot basidiomycetes on chemical composition and in vitro digestibility of oat straw and alfalfa stems. J. Anim. Sci. 70: 1292-1935.

Kayll, A.J. 1963. A technique for studying the fire tolerance of living tree trunks. Dept. For. Can. For. Res. Branch. Ottawa. No. 1012. pp. 22.

Kendrick, R. 1985. The Fifth Kingdom. Mycology Publications. Owen Sound, Ont. 364 pp.

Klopatek, C.C., L.F. Debano, and J.M. Klopatek. 1988. Effects of simulated fire on vesicular-arbuscular mycorrhizae in pinyon-juniper woodland soil. Plant and Soil 109: 245-249.

Kozlowski, T.T., and C.E. Ahlgren. 1974. Fire and Ecosystems. Academic Press. N.Y. 528 pp.

Le Tacon, F., J. Garbaye, and G. Carr. 1987. The use of mycorrhizas in temperate and tropical forests. Symbiosis 3: 179-206.

Lucarotti, C.J., C.T. Kelsey, and A.N.D. Auclair. 1978. Microfungal variations relative to post-fire changes in soil environment. Oecologia (Berl.) 37: 1-12.

Lundquist, J.E. 1993. Assessing Rhizina root disease hazard: a case study. S. A. For. J. 164: 51-53.

Maissurow, D.D. 1935. Fire as a necessary factor in the perpetuation of white pine. J. For. 33: 373-378.

Maissurow, D.K. 1941. The role of fire in the perpetuation of virgin forests in northern Wisconsin. J. For. 39: 201-207.

Malloch, D. and B. Malloch. 1981. The mycorrhizal status of boreal plants: Species from northeastern Ontario. Can. J. Bot. 59: 2167-2172.

Martinez-Amores, E., M. Valdes, and M. Quintos. 1990/1991. Seedling growth and ectomycorrhiae colonization of *Pinus patula* and *P. radiata* inoculated with spores of *Helvella lucunosa*, *Russula brevipes*, or *Lycoperdon perlatum*. New For. 4: 237-245.

Marx, D.H. 1969. The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathology. 59: 153-163.

Marx, D.H. 1991. The practical significance of ectomycorrhizae in forest establishment pp. 69-78 *in* the Marcus Wallenberg Foundation Symposia Proceedings: 7. Ecophysiology of Ectomycorrhizae of Forest Trees. The Marcus Wallenberg foundation. ISSN 0282-4647.

Marx, D.H., A.B. Hatch, and J.F. Mendicino. 1977. High soil fertility decreases sucrose content and susceptibility of loblolly pine roots to ectomycorrhizal infection by *Pisolithus tinctorius*. Can. J. Bot. 55: 1569-1574.

Mayfield, J.E. and D.D. Wade. 1993. Occurrence of macrofungi in burned and unburned hurricane-impacted loblolly pine forest. Proceedings of the 12th conference on fire and forest methodology. Oct 26-28. Clarion Resort Bucaneer, Jekyll Island, Georgia. SAF.

McAlpine, R.S. 1995. Testing the effect of fuel consumption on fire spread rate. PNFI. C.F.S. unpubl.

McCubbin, W.A. 1913. The morel. Ont. Nat. Sc. Bul. 8: 37-41

McGonigle, T.P., M.H. Miller, D.G. Evans, G.L. Fairchild, and J.A. Swan. 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phyt. 115: 495-501.

McRae, D.J. 1979. Prescribed burning in jack pine logging slash: a review. C.F.S. Info. Rep. 0-X-289.

Medve, R.J. and W.G. Sayre. 1994. Heavy metals in red pines, basidiomycete sporocarps and soils on bituminous stripmine spoils. J. Penn. Acad. Sci. 68: 131-135.

Meiklejohn, J. 1955. The effect of bush burning on the microflora of a Kenya upland soil. J. Soil Sci. 6: 111-118.

Menge, J.A., L.F. Grand, and L.W. Haines. 1977. The effect of fertilization on growth and mycorrhizae numbers in 11-year-old loblolly pine plantations. For. Sci. 23: 37-44.

Methven, I.R., and W.G. Murray. 1974. Using fire to eliminate understorey balsam fir in pine management. For. Chron. 50: 77-79.

Mikola, P. 1973. Application of mycorrhizal symbioses in forestry practice. pp. 383-411 *in* G.C. Marks and T.T. Kozolowski (eds.) Ectomycorrhizae: their ecology and physiology. Acad. Press, N.Y.

Molina, R. and J.M. Trappe. 1982. Patterns of ectomycorrhizal host specificity and potential among pacific Northwest conifers and fungi. For. Sci. 28: 423-458.

Morrall, R.A.A. and T.C. Vanterpool. 1968. The soil microfungi of upland boreal forest at Candle Lake, Saskatchewan. Mycologia 60: 642-654.

Nadelhoffer, K.J., J.D. Aber, and J.M. Melillo. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin (U.S.A.). Can. J. For. Res. 13: 12-21.

Ng, P.P., A.L.H Cole, P. Jameson, and J.A. McWha. 1982. Cytokinin production by ectomycorrhizal fungi. New Phytol. 91: 57-62.

Parke, J.L., R.G. Linderman, and J.M. Trappe. 1983. Effects of forest litter on mycorrhiza development and growth of douglas-fir and western red cedar seedlings. Can. J. For. Res. 13: 666-671.

Paul, E.A. and F.E. Clark. 1989. Soil microbiology and biochemistry. Academic Press. San Diego, CA. 275 pp.

Payette, S., C. Mornequ, L. Sirois, and M. Desponts. 1989. Recent fire history of the northern Quebec biomes. Ecology 70: 656-673.

Pera, J. and I.F. Alvarez. 1995. Ectomycorrhizal fungi of *Pinus pinaster*. Mycorrhiza. 5: 193-200.

Perrin, B. 1993. Public attitudes towards herbicides and their implications for a public involvement strategy for the Vegetation Management Alternatives Program: Executive summary. Burt Perrin Associates. Queens Printer. Toronto, Ontario. 11 pp.

Perry, D.A., M.P. Amaranthus, J.G. Borchers, S.L. Borchers, and R.E. Brainerd. 1989. Bootstrapping in ecosystems: internal interactions largely determine productivity and stability in biological systems with strong positive feedback. BioSci. 39: 230-237.

Petersen, P.M. 1970. Danish fireplace fungi: an ecological investigation of fungi on burns. Dan. Bot. For. 27: 6-97

Phillips, R. 1991. Mushrooms of North America. Little Brown and Company Ltd. Hong Kong. 319 pp.

Pliz, D.P. and D.A. Perry. 1983. Impact of clear cutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. Can. J. For. Res. 14: 94-100.

Raison, R.J. 1979. Modification of the soil environment by vegetation fires, with particular preference to nitrogen transformations: A review. Plant and Soil 51: 73-108.

Raubuch, M. and F. Beese. 1995. Pattern of microbial indicators in forest soils along an European transect. Biol. Fertil. Soils 19: 362-368.

Read, D.J. 1991. The role of the mycorrhizal symbiosis in the nutrition of plant communities pp. 22-37 *in* the Marcus Wallenberg Foundation Symposia Proceedings: 7. Ecophysiology of ectomycorrhizae of forest trees. The Marcus Wallenberg foundation. ISSN 0282-4647.

Reeves, F.B., D. Wagner, T. Moorman, and J. Kiel. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid West. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. Am. J. Bot. 66: 6-13.

Richards, B.N. 1961. Soil pH and mycorrhiza development in *Pinus*. Nature 190: 105-106.

Rippka, R. 1988. Isolation and purification of cyanobacteria. Met. Enzym. 167: 3-27.

Rowe, J.S. 1972. Forest regions of Canada. C.F.S., Pub. No. 1300. Petawawa, Ont.

St. John, T.V. and D.C. Coleman. 1983. The role of mycorrhizae in plant ecology. Can. J. Bot. 61: 1005-1014.

Seaver, F.J. and E.D. Clark. 1910. Studies in pyrophilous fungi - II. Changes brought about by the heating of soils and their relation to the growth of *Pyronema* and other fungi. Mycologia 1-2: 109-124.

Shaw, P.J.A., J. Dighton, J. Poskitt, and A.R. McLeod. 1992. The effects of sulphur dioxide and ozone on the mycorrhizas of Scots pine and Norway spruce in a field fumigation system. Mycol. Res. 96: 785-791.

Sinclair, W.A., D.M. Sylvia, and A.O. Larsen. 1982. Disease suppression and growth promotion in Douglas-fir seedlings by the ectomycorrhizal fungus *Laccaria laccata*. For. Sci. 28: 191-201.

Slankis, V., 1973. Hormonal relationships in mycorrhizal development pp. 231-298 *in* Marks, G.C. and Kozlowski, T.T. (eds.) Ectomycorrhizae: Their ecology and physiology. Academic Press, NY.

Smith, J.H.G. 1973. A review of the natural and managed roles of fire in the forests of British Columbia and in related areas. Part of an evaluation of the EDEN FIRE by D.B. Turner. Vancouver, B.C.

Soderstrom, B. 1991. The fungal partner in the mycorrhizal symbiosis pp. 54-68 *in* the Marcus Wallenberg Foundation Symposia Proceedings: 7. Ecophysiology of ectomycorrhizae of forest trees. The Marcus Wallenberg foundation. ISSN 0282-4647.

Springer, E.A. 1988. Forest Management Certificate Course. Prescribed burning. New Liskeard, Ont. OMNR. Northern Region.

SPSS 6.1 for Windows. 1994. SPSS Inc. Illinois, USA.

Stein, S.J., Price, P.W., Abrahamson, W.G. and C.F. Sacchi. 1992. The effect of fire on stimulating willow regrowth and subsequent attack by grasshoppers and elk. Oikos. 65: 190-196.

Theodorou, C. and G.D. Bowen. 1982. Effects of a bushfire on the microbiology of a South Australian low open (dry sclerophyll) forest soil. Aust. For. Res. 12: 317-327.

Tiwari, V.K., B. Rai. 1977. Effect of soil burning on microfungi. Plant and Soil. 47: 693-697.

Treu, R. and O.K. Miller Jr. 1993. Nuclear status of two *Suillus* species. Mycologia. 85: 46-50.

Trofymow, J.A. and R. van den Driessche. 1991. Mycorrhizas pp. 183-227 *in* R. van den Driessche (ed.) Mineral nutrition of conifer seedlings. CRC Press, Boca Raton, FL.

Van Wagner, C.E., 1970. Fire and red pine. Tall Timbers Fire Ecol. Conf. Proc. 10: 211-219.

Van Wagner, C. E. 1987. Development and Structure of the Canadian Forest Fire Weather Index System. C.F.S., For. Tech. Rep. 37.

Van Wagner, C.E. 1990. Six decades of forest fire science in Canada. For. Chron. 66: 133-137.

Van Wagner, C.E. and T.L. Picket. 1985. Equations and FORTRAN program for the Canadian Forest Fire Weather Index System. Agr. Can. C.F.S., Ottawa, Ont., For. Tech. Rep. 33. 1985\1987.

Vazquez, F.J., M.J. Acea, and T. Carballas. 1993. Soil microbial populations after wildfire. FEMS Microbio. Ecology 13: 93-104.

Vilarino, A. and J. Arines. 1991. Numbers and viability of vesicular-arbuscular fungal propagules in field soil samples after wildfire. Soil Biol. Biochem. 23: 1083-1087.

Villeneuve, N., Grandtner, M.M. and J.A. Fortin. 1989. Frequency and diversity of ectomycorrhizal and saprophytic fungi in the Laurentide mountains of Quebec. Can. J. Bot. 67: 2616-2629.

Visser, S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol. 129: 389-401.

Vogt, K.A. , D.A. Publicover, and D.J. Vogt. 1983. A critique of the role of ectomycorrhizas in forest ecology. Agric. Ecos. Environ. 35: 171-190.

Wade, D.D. 1989. A guide for prescribed fire in southwestern forests. USDA For. Ser., Southern Region, Tech. Pub. R8-TP11.

Waller, K. and R. Agerer. 1993. Ectomycorrhizae of *Dermocybe cinnamomeolutea* (Cortinariaceae) and *Tricholoma acerbum* (Tricholomataeceae). Sentnera, Mitteilungen der Botanischen Staatssammlung und des Instituts-fur Systemattische Botanik der Universitat Munchen. 1: 23-38.

Warcup, J.H. 1990. Occurrence of ectomycorrhizal and saprophytic discomycetes after a wild fire in a eucalypt forest. Mycol. Res. 94: 1065-1069.

Weber, M.G. 1990. Response of immature aspen ecosystems to cutting and burning in relation to vernal leaf-flush. For. Ecol. Man. 31: 15-33.

Weber, M.G., M. Hummel, and C.E. Van Wagner. 1987. Selected parameters of fire behaviour and *Pinus banksiana* Lamb. regeneration in eastern Ontario. For. Chron. 63: 340-346.

Weber, M.G. and S.W. Taylor. 1992. The use of prescribed fire in the management of Canada's forested lands. For. Chron. 68: 324-334.

Wein, R.W. and D.A. MacLean. 1983. An Overview of fire in Northern ecosystem spp.1-15 *in* Wein, R.W. and D.A. MacLean (eds.) Scope 18: The role of fire in Northern circumpolar ecosystems. John Wiley and Sons. Toronto, Ont.

Wells, C.G., R.E. Campbell, L.F. DeBano, C.E. Lewis, R.L. Fredriksen, E.C. Franklin, R.C. Froelich, and P.H. Dunn. 1979. Effects of fire on soil. USDA. For. Ser. Gen. Tech. Rep. WO-7.

White, C.S. 1986. Effects of prescribed fire on rates of decomposition and nitrogen mineralization in a ponderosa pine ecosystem. Biol. Fertil. Soils. 2: 87-95.

Wicklow, D.T. 1975. Fire as an environmental cue initiating ascomycete development in a tallgrass prairie. Mycologia. 67: 852-861.

Wicklow, D.T. and B.J. Hirschfield. 1979. Competitive hierarchy in post-fire ascomycetes. Mycologia 70: 47-54.

Widden, P., and D. Parkinson. 1975. The effects of a forest fire on soil microfungi. Soil Bio. Biochem. 7: 125-138.

Wilton, W.C., and C.H. Evans. 1974. Newfoundland fire history 1619-1960. C.F.S. Info. Rep. N-X-116.

Wright, E., and W.B. Bollen. 1961. Microflora of Douglas-fir soil. Ecology 42: 825-828.

Wright, H.E., Jr., and M.L. and Heinselman. 1973. The ecological role of fire in natural conifer forests of western and northern North America. Quat. Res. 3: 319-328.

Wright, E., and R.F. Tarrant. 1958. Occurrence of mycorrhizae after logging and slash burning in the Douglas-fir forest type. U.S. For. Serv. Pac. Northwest For. Range Exp. Stn. Res. No. PNW-160. 7 pp.

Zak, J.C., and D.T. Wicklow. 1980. Structure and composition of a post-fire ascomycete community: role of abiotic and biotic factors. Can. J. Bot. 58: 1915-1922.

Appendix A

PNFI Seedlot Viability and Testing Date Information

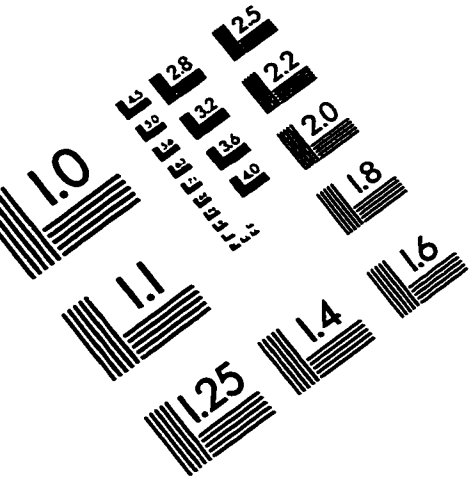
Germination data for *P. strobus* seeds: Seedlot number, viability, and year tested for seeds from the Petawawa National Forestry Institute.

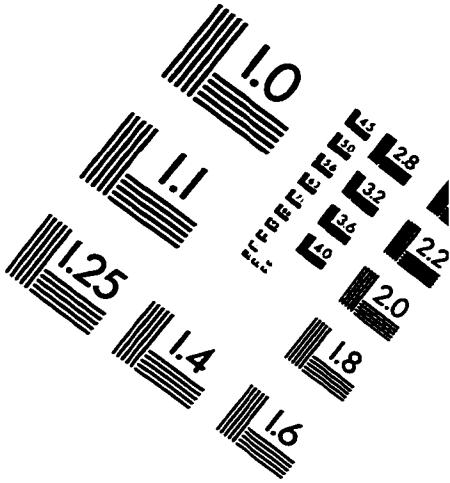
Seedlot Number	Percent Viability (%)	Year Tested
8930576	98	1990
8930577	97	1990
9230120	96	1990
9230121	98	1992
9230122	98	1993
9230123	98	1993

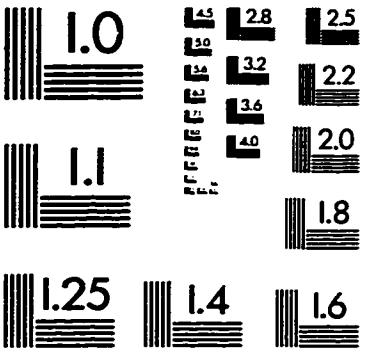
Germination data for *P. resinosa* seeds: Seedlot number, viability, and year tested for seeds from Algonquin Park and Cedar Lake.

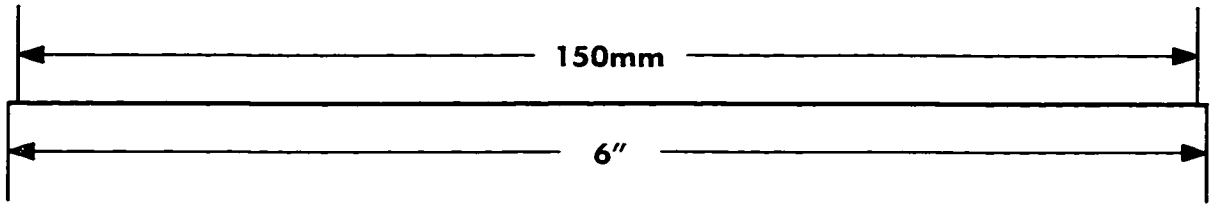
Seedlot Number	Percent Viability (%)	Year Tested
9230449	97	1993
9230450	100	1993

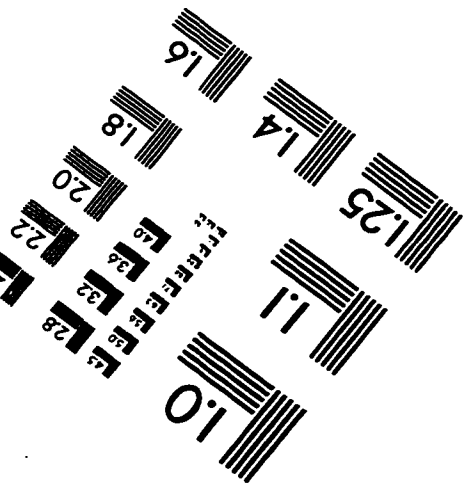
IMAGE EVALUATION TEST TARGET (QA-3)

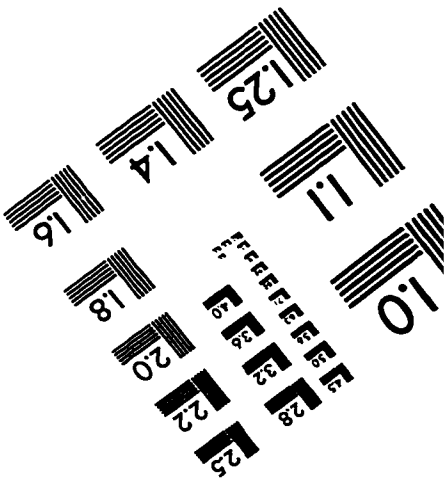












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